JOURNAL OF THE ARNOLD ARBORETUM

HARVARD UNIVERSITY VOLUME 71 NUMBER 1

ISSN 0004–2625

Journal of the Arnold Arboretum

The *Journal of the Arnold Arboretum* (ISSN 0004-2625) is published quarterly in January, April, July, and October for $70.00 per year, plus $10.00 or $15.00 postage for addresses outside of the United States, by the Arnold Arboretum of Harvard University. It is printed and distributed by Allen Press, Inc., 1041 New Hampshire Street, Lawrence, Kansas 66044. Second-class postage paid at Lawrence, Kansas. POSTMASTER: send address changes to *Journal of the Arnold Arboretum*, % Allen Press, Inc., P.O. Box 368, Lawrence, Kansas 66044.

Subscriptions and remittances should be sent to *Journal of the Arnold Arboretum*, 1041 New Hampshire Street, Lawrence, Kansas 66044, U.S.A. Claims will not be accepted after six months from the date of issue.

Volumes 1–51, reprinted, and some back numbers of volumes 52–56 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U.S.A.

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COVER: The stylized design appearing on the Journal and the offprints was drawn by Karen Stoutsenberger.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

IMPORTANT NOTICE

After the final issue of volume 71, the *Journal of the Arnold Arboretum* will suspend publication pending a comprehensive review of its role in supporting the mission of the Arboretum. In 1988 the Arnold Arboretum underwent administrative review following the resignation of Dr. Peter Ashton as director. This led to a reaffirmation of its mission by the President and Fellows of Harvard College (the Corporation; see mission statement on facing page). It also led to changes in its administrative position within Harvard University and a subsequent search for a new director, who assumed the position in January 1989. In addition, the Harvard University Herbaria (of which the collections of the Arnold Arboretum are a part) are presently going through a period of staff and faculty transition. Consequently it has seemed prudent to suspend publication of a journal that was originally intended to serve the mission of the Arnold Arboretum as an organ "to publish within a reasonable time the material which is gathered in its laboratories."[1]

During the next two years, the research mission of the Arnold Arboretum will be undergoing review and clarification. The shape of systematic and botanical scholarship within Harvard's academic departments will become clear as new staff and faculty are hired. At this future point, the potential supporting role of an in-house journal will be assessed. If the *Journal* can further the scholarly mission of the Arboretum, publication will be resumed. During the suspension, the Arnold Arboretum will continue to support publication of the Generic Flora of the Southeastern United States.

I will be happy to address the queries and concerns of subscribers about this suspension of publication.

Robert E. Cook
Director and Arnold Professor

[1] C. S. Sargent, Introduction, *Journal of the Arnold Arboretum*, Vol. 1, p. [i], 1919.

THE MISSION OF THE ARNOLD ARBORETUM

The Arnold Arboretum is held in trust by Harvard University according to the terms of the Indenture of Trust of 1872. This legal document provided for the creation of the living collections as a practical demonstration of the variety of plants that could be grown in this climate. It also mandated the appointment of the Arnold Professor to manage the Arboretum and to teach the knowledge of trees and related topics.

Although there have been many significant changes in the fields of botany and horticulture and the Arnold Arboretum itself has fulfilled many different purposes during the past century, the basic premises of the Indenture still hold. It is most appropriate to reemphasize the traditional strengths of the Arnold Arboretum through a strong focus on botany and horticulture.

The mission of the Arnold Arboretum may be outlined as follows:

(1) to develop, curate, and maintain a well-documented collection of living woody plants from around the world that are hardy in the Boston area;

(2) to study these plants and their relatives and associates in nature through the maintenance of a herbarium and library and through directly related research in botany and horticulture;

(3) to provide instruction in botany, horticulture, dendrology, and other fields related to the living collections.

As part of the City of Boston's park system, the Arboretum's Jamaica Plain site functions as an outdoor museum open to the public. The highest priority of the Arboretum's administration is the proper curation and maintenance of these living collections. Proper curation includes acquisitions through field expeditions and exchanges with other institutions as well as cultivation and propagation of existing specimens to enhance and maintain the scientific and instructional value of the collections.

The second priority of the Arboretum, the study of its collections and their relatives and associates in nature, directly benefits the curation of the collections. The preserved collections and the library are indispensable tools for this research, and their curation and maintenance are therefore essential. All of the Arboretum's resources— the living collections, the preserved collections, and the library—are available for scholarly research. The director of the Arnold Arboretum is responsible for ensuring that adequate and up-to-date materials are available for present and future scholars to teach and to pursue research in the areas represented.

Educational programs are the Arboretum's third-highest priority. The Arnold Arboretum offers a variety of programs for public instruction in horticulture, botany, dendrology, and landscape gardening and, in addition, disseminates knowledge of plants through its publications. The director and Arboretum professional staff may also offer courses, as appropriate, within other academic programs of Harvard University.

—Document approved by the Harvard Corporation, February 1988.

JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 71 JANUARY 1990 NUMBER 1

THE GENERA OF BETULACEAE IN THE SOUTHEASTERN UNITED STATES[1]

JOHN J. FURLOW[2]

BETULACEAE S. F. Gray, Nat. Arr. Brit. Pl. **2**: 243. 1821, "Betulideae," nom. cons.

(BIRCH FAMILY)

Small to large, columnar or pyramidal to spreading deciduous trees or shrubs; sap watery; branching excurrent to deliquescent; trunks and branches terete to irregularly longitudinally fluted, the branchlets terete, slender, often distichous, uniform or differentiated into long and short shoots. Bark close or exfoliating

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8415637 (Norton G. Miller, principal investigator), under which this account was prepared, and BSR-8415769 (Carroll E. Wood, Jr., principal investigator). This treatment, the 130th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. Those references I did not verify are marked with asterisks.

The illustrations were prepared by Arnold D. Clapman under an earlier grant from the National Science Foundation. Carroll Wood or Kenneth R. Robertson made the dissections and supervised the drawings. The materials used were from plants in the Arnold Arboretum, as well as from wild plants, with additional items from the Arnold Arboretum and Gray herbaria (A, GH). Dr. Elizabeth Wood collected some of the specimens for the illustration of *Alnus*.

I extend my sincere thanks to Norton Miller and Carroll Wood for their help, encouragement, and patience throughout this study. I am especially grateful to Dr. Wood for overseeing the preparation of the drawings and for sharing his preliminary bibliography of the Betulaceae with me, and to Dr. Miller for providing me with funds to travel to the New York State Museum to study herbarium material there. Drs. Wood and Miller have both read the manuscript and have made many useful suggestions. Bruce P. Dancik, Peter R. Crane, and Thomas G. Lammers have also read and commented on the manuscript. I am thankful to them, and also to the many others with whom I have discussed aspects of this work.

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in thin layers, thin, smooth, often marked with prominent lenticels, sometimes becoming thick, corky, and rough, furrowed or scaly with age, often strongly tanniferous; young twigs glabrous to pubescent, sometimes covered with resinous glands, terminal buds lacking; leaf scars raised, with 3 vascular bundle scars; winter buds stipitate or sessile, narrowly to broadly ovoid, terete or sometimes angular in cross section, divergent, held parallel to the twig, or appressed, acute to rounded at apex, covered with 2 smooth, valvate (stipular) scales or few to many smooth or longitudinally striate imbricate ones [or occasionally naked]; nodes trilacunar; wood light brown to nearly white, diffuse porous, close grained, moderately soft to very hard; pith relatively small, homogeneous, triangular to circular in cross section. Leaves simple, petiolate, alternate, spirally arranged, 3-ranked to distichous; blades ovate to deltoid, elliptic, obovate, or suborbicular, coarsely to finely toothed, glabrous to sparingly pubescent adaxially, glabrous to tomentose and sometimes covered with resinous glands abaxially; venation pinnate, the secondary veins craspedodromous [or semicraspedodromous], divergent and straight to strongly ascending, the tertiary (cross) veins usually prominent; leaves conduplicate in bud, open and convex but becoming conduplicate as they expand, or open and concave; stipules present, free, broadly ovate to narrowly linear, deciduous. Plants monoecious, the flowers imperfect, anemophilous, much reduced. Inflorescences consisting of pendulous or erect catkins of reduced, 3-flowered cymules, or reduced to compact clusters of several minute flowers (florets); staminate catkins terminal or lateral on the branchlets, borne on either long or short shoots, solitary or in small to large racemose clusters, precocious [or developing during the current season], when formed the previous season exposed or enclosed in buds during the winter, elongate, cylindrical, pendulous, conspicuously bracteate, the scales and flowers densely to loosely arranged, the scales consisting of [(1–)]3–5 fused bracts; carpellate inflorescences terminal or lateral on the branchlets, borne on either long or short shoots, solitary or in small [to large] racemose clusters, precocious or developing during the current season, when formed the previous season exposed or enclosed in buds during the winter, consisting of short to moderately long, erect to pendulous, bracteate catkins or of small, compact clusters of flowers subtended by leafy involucres; scales and flowers densely to loosely arranged, the bracts [(1–)]3–5 per scale, becoming variously fused and often large and subfoliaceous or woody in the infructescences. Staminate flowers small, the perianth lacking or of 1–4(–6) minute tepals; stamens (1–)4(–6), in 1 whorl, sometimes appearing to be more due to development of part or all of additional flowers of the reduced cymule; filaments short, separate or partially to wholly connate, or sometimes divided part or all the way to the base; anthers tetrasporangiate, 2-locular, dorsifixed, extrorse, entire or partially to wholly divided from the apex, opening by longitudinal slits; pollen grains smooth or slightly granular, spheroidal to oblately flattened, angular, 15–45 μm in diameter, aspidote, poroid, the apertures (3 or) 4–7, circular to elliptic, equatorial, evenly spaced; rudimentary gynoecium usually absent. Carpellate flowers small, perianth usually lacking or highly reduced and adnate to the ovary; ovary compound, of 2 (or 3) carpels, inferior or nude (i.e., apparently inferior on the basis of vascular traces, but lacking a

perianth), 2- (or 3-)locular below, unilocular above, with 2 (or 3) linear styles, these stigmatic above; ovules axile, 1 or 2 per locule, pendulous, anatropous, crassinucellar, unitegmic or bitegmic; staminodes usually absent; fertilization chalazogamous; endosperm nuclear, becoming cellular. Infructescences woody and strobiluslike or consisting of elongate to compact or irregular foliaceous clusters, the scales (bracts) persistent or deciduous, variously lobed and toothed. Fruits nuts, nutlets, or 2-winged samaras (sometimes with the wings reduced), maturing and dispersed the same season as or the season following pollination. Seed single, pendulous; endosperm present but thin at maturity; embryo large, straight, as long as the seed, the cotyledons small and flat, or greatly thickened, plano-convex, and oily; radicle superior. Embryo-sac development of the Polygonum type. Germination epigeal or hypogeal. Base chromosome numbers 7, 8. (Including Corylaceae Mirbel, Elem. **2:** 906. 1815, nom. cons., and Carpinaceae Kuprianova, Taxon **12:** 12. 1963.) TYPE GENUS: *Betula* L.

A family of six genera and about 150 species, primarily of the boreal and cool-temperate zones of the Northern Hemisphere, but also represented at high elevations from Mexico southward through Central America to northern Argentina. Despite its small size, the family includes dominant trees of forests of temperate Asia, northern Europe, northwestern North America, mountainous parts of Mexico, Central America, and northern South America, and the circumboreal region. Five of the genera occur in North America and are represented by one or more species in the southeastern United States. The remaining genus, *Ostryopsis* Decne. (most closely related to *Corylus* L.), consists of two species of shrubs restricted to northern and western China.

The Betulaceae are woody plants easily distinguished by their simple, pinnately veined, usually ovate, sharp-toothed leaves, their long, dense staminate catkins that often develop the season before anthesis, and (except in *Corylus* and *Ostryopsis*) their strobiluslike infructescences. The family is held together on the basis of many characters, including habit; leaf structure, venation, and arrangement; trichome morphology; wood anatomy; inflorescence morphology; ovary structure; ovule morphology and position; pollen morphology; embryo structure; chalazogamous fertilization; germination pattern; and serological reactions.

The Betulaceae are usually treated as a single family closely allied with the Fagaceae and placed with it in the order Fagales, although Hjelmqvist (1957, 1960) and Takhtajan (1969, but not 1980) placed the family in its own order, Betulales, on the basis of embryological differences, especially the presence of endosperm in the Betulales (since then shown to exist in both groups, as discussed below). The earliest natural post-Linnaean systems treated the genera of the Betulaceae, together with the elms, oaks, willows, and other amentiferous trees, as members of a single large assemblage (e.g., "Castaneae" of Adanson, "Amentaceae" of Jussieu). Adanson segregated the betulaceous and fagaceous genera into one of three "sections" of the Castanieae, corresponding to the modern Fagales. In most of the important subsequent work until that of Prantl (e.g., De Candolle; Regel (1861, 1868); and Spach (1841, 1842a–c)), the group was divided into two families, Betulaceae and Corylaceae Mirbel, following

the lead of Linnaeus, who had placed *Betula* (including *Alnus* Miller) in the Monoecia Tetrandia, and *Carpinus* (including *Ostrya* Scop.) and *Corylus* in the Monoecia Polyandria. De Candolle, in his monograph of the Corylaceae, further divided that family into two tribes, Coryleae Meisner and Carpineae Döll. However, Prantl treated the entire group as a single family, Betulaceae, composed of two tribes, Coryleae Meisner and Betuleae, the system followed by Winkler in the most recent family monograph. Koehne also adopted this arrangement, but he elevated the tribes to subfamily status; this treatment has been accepted by a number of modern authors, including Jury, Rendle, Takhtajan (1980), and Thorne (1983). Bentham & Hooker combined the Betulaceae and Fagaceae into the single family Cupuliferae, in part based on a misunderstanding of the nature of the bracts subtending the fruits in these families (Abbe, 1974), but few have followed this path. The family is still sometimes divided into two families, the Betulaceae and the Corylaceae, and Kuprianova has proposed the further splitting of the Coryloideae into two families, Corylaceae and Carpinaceae, following De Candolle's tribes Coryleae and Carpineae. Particularly in Europe, the two-family scheme has been adopted by many authors, including Airy Shaw in Willis, Dahlgren (1975, 1977, 1980, 1983), Hjelmqvist (1957, 1960), Hutchinson (1959, 1967), and Jury. In America, it has been used by Mohlenbrock & Thomson, Rehder (1940), and Small (1903, 1933). Some of these treatments based recognition of two families in part on the belief that a fundamental difference exists in the staminate inflorescences of the two groups (there being three flowers, each consisting of one to six stamens per bract in the Betulaceae, and one flower, consisting of many stamens per bract in the Corylaceae). However, it has now been established that no such difference in staminate inflorescence structure exists in these two groups (see below). Most modern authors (e.g., Cronquist, 1981, 1988; Melchior; Takhtajan (1969, 1980); and Thorne, 1968, 1973, 1983) maintain the family as a single group. When one family is recognized, the name Betulaceae is conserved against Corylaceae.

The Betulaceae are treated here as consisting of a single family subdivided into two natural subfamilies, the Betuloideae and the Coryloideae (Regel) Koehne, these corresponding to the tribes Betuleae and Coryleae recognized by Prantl and Winkler. To reflect the substantial differentiation between *Carpinus* and *Ostrya* Scop. on the one hand, and *Corylus* and *Ostryopsis* on the other, the Coryloideae are further divided into two tribes, the Coryleae and the Carpineae Döll.

In an early analysis of generic affinities within the family, Anderson & Abbe found that species differences are consistently smaller than generic differences and are approximately equal from genus to genus. These authors noted an exception, however, in the case of *Carpinus* and *Ostrya,* which they concluded show less divergence than occurs among some of the subgroups within the genus *Betula.*

Where best to place the Betulaceae within the angiosperms has been a source of continuing disagreement, in part because of an unclear fossil record of the ancestors of the group. The Englerian tradition, following earlier authors such as Jussieu, placed the amentiferous families together in a relatively low position in the dicotyledons (see Stern). Bessey, perhaps in an overreaction to the ap-

parent phylogenetic inaccuracy of the Englerian arrangement, gave the Betulaceae an exaggeratedly advanced level (in the Sapindales). Cronquist (1981, 1988), Melchior, Takhtajan (1969, 1980), and Thorne (1973, 1983) all placed the Fagales, along with other "core" orders of the Amentiferae, in a position more advanced than the magnoliids, less advanced than the rosids, and with close ancestral ties to the Hamamelidales. Dahlgren, in his early treatments (1975, 1977), adopted a similar scheme but placed the Hamamelidanae somewhat nearer the rosid groups. However, in the most recent versions of his system (1980, 1983), he joined the Fagales with the Juglandales, Saxifragales, and Rosales in the Rosiflorae. Taking a radically different view, Meeuse (1975a–c) maintained that the Amentiferae, including the Betulaceae, were not derived from a group having well-developed flowers but instead represent a fundamentally distinct line of evolution in the flowering plants. However, this position has received little acceptance.

There is disagreement on the phylogenetic arrangement of genera in the family. While virtually all authors recognize a fundamental dichotomy between the Betuloideae and the Coryloideae, and most believe the Betuloideae to be the less specialized, the arrangement of the genera within these groups is unsettled. Within the Betuloideae, *Betula* has traditionally (e.g., by Bentham & Hooker; Komarov; Prantl; Regel (1861, 1868); Spach (1841); Winkler) been placed before *Alnus*. However, modern workers (e.g., Furlow, 1979, 1983a; Hall; Kikuzawa; Takhtajan, 1969, 1980) generally consider *Alnus* the less specialized, and it has been treated accordingly in a number of recent floras (e.g., those by Scoggan; Soper & Heimburger; Voss). In the Coryloideae there is more confusion, and all possible arrangements of the four genera are found in the modern literature. Winkler, in part following Prantl, viewed *Ostryopsis* as most primitive, *Ostrya* and *Carpinus* as intermediate, and *Corylus* as most advanced. Bentham & Hooker and Hutchinson (1959, 1967), on the other hand, listed *Carpinus* as least specialized, followed by *Ostryopsis, Ostrya,* and *Corylus*. On the basis of wood anatomy and leaf and bud structure, respectively, Hall and Kikuzawa considered *Corylus* to be the most primitive and *Carpinus* the most advanced, a view first proposed by Tippo. Hjelmqvist (1948), from floral and fruit structure, and Hardin & Bell, on the basis of trichome morphology, viewed *Carpinus* as the most primitive and *Corylus* as the most advanced. Obviously, a detailed examination of this problem is needed. In a preliminary cladistic study using many features of a variety of types, Furlow (1983a) concluded that *Carpinus* was the least specialized, followed by *Ostrya* and *Ostryopsis,* with *Corylus* the most specialized.

The leaves of the Betulaceae are simple and pinnately veined, with nonglandular teeth of a modified urticoid type (L. J. Hickey & Wolfe). The secondary veins are generally characterized as uniformly craspedodromous (L. J. Hickey; L. J. Hickey & Wolfe). However, venation in members (mostly Asian) of *Alnus* subg. Clethropsis (Spach) Regel is semicraspedodromous (Furlow, 1979), a unique condition in the Fagales, although the phylogenetic significance of this pattern has not been investigated. The basal secondary veins tend to be crowded in most genera of the family, especially in *Corylus* (Meyerhoff). Branches of the lower secondary veins ("outer secondaries") appear in all genera and

run, like the secondaries, to teeth at the margin; regular and usually prominent tertiary veins connect the secondaries.

The general structure of vegetative features in the family has been treated by Boubier, Metcalfe & Chalk, and Solereder. The leaves of all genera are pubescent abaxially, although in individual species or populations they vary from glabrous to densely tomentose. Most betulaceous leaves have at least some hair, especially along the major veins and in the axils of the secondary veins. Hardin & Bell have studied the foliage of the five North American genera of the family in detail and have identified six distinct trichome types, including unicellular and multicellular hairs of several kinds, stipitate glands, and peltate scales (sessile glands). The four hair types are found in all five of the genera, tying the family together as a unit (Hardin & Bell). Most of these trichome types are also present in the Fagaceae (Hardin & Johnson), suggesting a close relationship between the Betulaceae and the Fagaceae. Large glands are frequent on the leaves and twigs of *Alnus* and *Betula* (Bell *et al.*; Furlow, 1979). It has been shown by Dorman that in *Alnus* these glands secrete a high-molecular-weight polyterpene and by Wollenweber that their product includes flavonoid compounds.

Several authors have sought the origin and phylogeny of the Betulaceae in the structure of their flowers and inflorescences (Abbe, 1935, 1938; Hjelmqvist, 1948; Korchagina) and in their embryology (Benson; Hjelmqvist, 1957; Nawaschin). In a comprehensive investigation of the floral and inflorescence anatomy and morphology of the family, Abbe (1935, 1938) proposed that the inflorescences consist of systems of reduced three-flowered cymules and hypothesized the loss of various bracts, flowers, and flower parts in various genera, leading to the present patterns. He argued (1935), on the basis of the position of the tepals or their vestigial vascular traces, that the ovaries of all members of the family are inferior, and he proposed that the bicarpellate ovaries of the various genera have arisen in several different ways: those in *Alnus, Betula,* and *Corylus* from loss of the carpel in the radius of the adaxial tertiary bract; those in *Carpinus* and *Ostrya* from loss of the carpel in the radius of the secondary bract. Hjelmqvist (1948) disagreed with the latter interpretation, concluding that the different positions noted were probably due only to twisting of the original transverse carpels. In a third paper Abbe (1974) reviewed the floral structure of the entire Amentiferae and argued that the Betulaceae form a single evolutionary unit with three clearly divergent lines, which he assigned to the tribes Betuleae, Carpineae, and Coryleae.

The distinctive ways in which individual catkins are clustered in various genera and infrageneric groups of the Betulaceae have been discussed by Furlow (1979), Hjelmqvist (1948), Jäger, and Murai. Jäger, expanding upon the ideas of Hjelmqvist (1948), proposed that the hypothetically ancestral synflorescence of the family consists of an axis bearing a terminal cluster of staminate catkins, with lateral clusters of carpellate catkins placed below it. This type resembles the form seen today in members of *Alnus* subg. CREMASTOGYNE Schneider in Sarg. and, in somewhat reduced form, *Alnus* subg. ALNUS. Jäger has traced the evolution of various synflorescence types occurring in most extant betulaceous genera, explaining their progressions by means of translocations of the shoot

innovations into the synflorescence itself, tendencies to monopodial or sympodial proliferation of the synflorescence, reduction in size and number of catkins, and winter protection of carpellate catkins by bud scales. He has also shown that these changes correlate closely with vegetative adaptations related to severity of climate. In *Alnus* subg. ALNOBETULA Peterm., as well as in most subgroups of *Betula,* the tendency has been toward a monopodial form with a terminal staminate cluster, the carpellate clusters being held on lateral shoot innovations. However, in *Betula* sect. HUMILES W. D. Koch the axes have diversified sympodially and have been reduced to a form in which solitary staminate catkins occupy a position below the carpellate ones on lateral short shoots. Sympodial modifications and reductions are seen as well in *Carpinus* and *Ostrya.* In *Carpinus* the solitary or clustered staminate catkins are located laterally below the terminal carpellate ones, while in *Corylus* this trend reaches its ultimate configuration: the staminate clusters are positioned laterally below reduced solitary carpellate inflorescences.

The Betulaceae are generally uniform in fruit structure, but each genus has distinctive modifications associated with dispersal by means of wind, water, or animals. The tiny, lateral-winged samaras of *Alnus* and *Betula* are carried great distances and in large numbers by air currents. In certain species of *Alnus,* these wings have been reduced or lost and the fruits are apparently dispersed mostly by water; they have been shown to float for long periods (McVean). The fruits of *Carpinus* and *Ostrya* are also scattered by wind, but with the aid of greatly expanded bracts rather than wings on the fruits themselves. The fruits of these genera are widely called both achenes and nutlets, but since their walls are quite bony and tightly attached to the enclosed seed, the latter is more appropriate (see Hjelmqvist, 1948). The most striking fruit modifications of the Betulaceae are seen in the dramatic adaptations of *Corylus* fruits for zoöchory (Stebbins; Stone).

The seeds of all the genera are similar in internal structure (with axile and investing embryos), a type regarded as advanced in the angiosperms (A. C. Martin). In the Betuloideae the embryos are somewhat less investing than in the Coryloideae, and thus they may be considered less specialized. In both groups several ovules are initially laid down (Hagerup), but only one of these develops. In the Coryloideae (as well as in the Fagaceae (Benson; Hjelmqvist, 1948)), but not in the Betuloideae, several embryo sacs may develop.

The wood of the Betulaceae has been studied by Bailey (1910, 1911, 1912), Forsaith, Hall, Hoar, and others. Bailey (1911) discussed the presence of aggregate rays in the wood of the Betulaceae and related families and proposed a phylogenetic series involving the development of large multiseriate rays from uniseriate ones. In a second paper (1912) he developed this concept further and demonstrated reversals to uniseriate rays in various species. Hoar concluded, on the basis of the presence of aggregate rays, that the family was extremely primitive in the dicots. A study of the wood anatomy of the Betulaceae by Hall showed the family to be "anatomically natural and closely knit" (p. 262) but with clear distinctions between the Betuloideae and Coryloideae. However, Hall did not speculate on whether these groups should be considered one family or two. He found the Betuloideae to be more primitive than the

Coryloideae in having relatively large vessels lacking spiral thickenings and having scalariform perforation plates. He also concluded that true tracheids were present in the Betuloideae and absent in the Coryloideae. However, Kasapligil and Yagmaie & Catling have shown the wood of *Carpinus* and *Corylus* to contain tracheids. Within the Betuloideae *Alnus* was seen by Hall as less specialized than *Betula* in terms of the number and spacing of the bars of the perforation plates and in the presence of opposite, as well as alternate, intervascular pitting. Within the Coryloideae he noted a trend of specialization leading from *Corylus* to *Carpinus* and then to *Ostrya,* this involving reduction in the number of bars of the perforation plates, an increased presence of spiral thickenings on vessel walls, and other characters.

Brunner & Fairbrothers concluded from serological investigations of the six genera (but based on very limited sampling) that these groups held together well and should be treated as a single family. Petersen & Fairbrothers showed the Betulaceae as a whole to be closely related to members of the Fagaceae, Myricaceae, and Juglandaceae on serological grounds, with members of the Anacardiaceae, Aceraceae, Moraceae, Oleaceae, and other families of rosid affinity forming a very distant group. Other than this, there is little positive chemical evidence demonstrating relationships between the Betulaceae and other amentiferous families (Mears).

The Betulaceae are well known cytologically (Jaretzky; Wetzel, 1927, 1928, 1929; Woodworth, 1929a–c, 1930a, b, 1931). Chromosomally, the family consists of groups that do not correspond to the tribes or subfamilies (Raven). The base chromosome number of *Betula* and *Corylus* is 14, while that of *Carpinus, Ostrya,* and *Ostryopsis* is eight. *Alnus,* usually placed in the $x = 14$ group with *Betula* and *Corylus,* was suggested by Furlow (1979), after a count by Chiba, to have a base number of seven, the probable original base number of the Fagales (Raven). This number had previously been predicted for the family by Woodworth (1931) and by Wanscher. An allozyme study of *A. viridis* subsp. *crispa* ($2n = 28$) by Bousquet and colleagues (1987) indicated that this species could be treated either as a diploid or a diploidized autotetraploid. Additional study of *A. incana* subsp. *rugosa* by these authors also revealed diploidlike expression for all polymorphic allozyme loci (Bousquet *et al.,* 1988), and additional indirect evidence for a base number of seven has been provided by Brown & Al-Dawoodie, who found that meiotic behavior in hybrid birches suggests that $2n = 42$ trees actually represent hexaploids.

The Betulaceae are an ancient group, extending back in the fossil record to the Upper Cretaceous on the basis of both leaves and pollen. Fossils assigned to the family become abundant in strata of Paleocene and Eocene age in both the New and the Old worlds. This record has been summarized by Crane (1981), Crane & Stockey, Crepet, and Wolfe (1973). Members of the Betuloideae first occur in the Upper Cretaceous (Maestrichtian); coryloid types in the lower Paleocene. Evidence that *Betula* had diverged from *Alnus* by the mid-Eocene is provided by Crane & Stockey, and fossil evidence from northwestern North America indicates that the subgenera of *Alnus* had differentiated and were present in the New World during the Miocene if not before (Wolfe, 1969).

The ancestor of the Betulaceae is not obvious from the features of other

extant families. On the basis of floral structure, Abbe (1938) tentatively suggested the Fagaceae as the most likely candidate, but in spite of the similarities, there are important differences between the two families, including the structure of the carpellate inflorescences and the presence of a "stem cupule" around the fruits. Takhtajan (1969) believed that the Betulaceae share a common ancestry with the Fagaceae but are not derived directly from them. Hjelmqvist (1948) concluded that the Betulaceae are not closely related to the Fagales, but that they show significant connections to the Juglandaceae in floral coalescence, chalazogamy, and other basic features. He believed that the two major subgroups of the family are closely related, although one probably did not originate directly from the other: the distinctive lines of specialization within each group, such as differences in the fruits and the involucre, indicated rather that they had developed from a common ancestor.

Tippo first suggested that the Betulaceae may have been derived from hamamelidaceous stock, and many modern workers have adopted this position. Endress (1967, 1977) emphasized that the Hamamelidales combine features of the mainly insect-pollinated Cunoniales and Rosales with those of the wind-pollinated Fagales and argued that the Betulaceae and Fagaceae may be derived from a *Corylopsis*-like hamamelid ancestor. Ehrendorfer concluded that the Hamamelidae, including the Hamamelidales and the Fagales, can be regarded as remnants of an ancient stock of dicots linking the Magnoliidae and the Rosidae-Dilleniidae, but with tendencies toward anemophily and floral reduction.

Doyle has suggested that the ancestor of the more advanced Hamamelidae (including the Betulaceae) may have been a member of the Normapolles complex, known from its psilate, complex-walled, tricolporate pollen, which first appeared during the Cretaceous and reached a peak in the Santonian, and which seems to have been adapted for wind pollination. However, the pollen of modern Betulaceae is much more specialized than that of the modern Hamamelidales (L. J. Hickey & Doyle; Walker & Doyle). This has been used to support the view that some groups of modern Amentiferae (e.g., the Juglandaceae) may have a rosid, rather than a hamamelid, ancestor.

There is fossil evidence that the unlobed, pinnately veined leaves of the Hamamelidae are of secondary derivation from a platanoid ancestor with palmately veined and lobed leaves (L. J. Hickey & Wolfe; Wolfe, 1973). In *Corylus* the basal secondary veins often tend toward an actinodromous condition, rising abruptly toward the apex, where there is a suggestion of lobing. This intriguing pattern (which can sometimes also be seen to varying degrees in other Betulaceae—e.g., in *Alnus viridis* subsp. *sinuata* (Rydb.) Löve & Löve) resembles that of the hamamelidaceous *Corylopsis* (Wolfe, 1973) and may represent a remnant of a primitive venation pattern. However, such venation is also explicable by relatively minor structural adjustments to the ordinary form of the extant Fagales (similar distortions to the apical parts of the leaves of several species of *Alnus* have been reported by Furlow, 1979). Kasapligil (p. 85) explained the pattern in *Corylus* as "due to the auriculate condition of the cordate [base] of blades and the abrupt acuminate form of the leaf apices." Wolfe (1973) pointed out that in toothed primitive Juglandaceae, the secondary

veins vary from a craspedodromous pattern, the teeth being entered along the apical side by a branch from the secondary vein. He concluded (p. 351) that these leaf features "do not conform to any known specialization of venation elsewhere in the Hamamelididae but rather are highly similar to members of Rosidae." The similar pattern in *Alnus* subg. CLETHROPSIS may provide a significant connection. Wolfe thought that, although the paleobotanical and palynological evidence favors a Normapolles ancestor for the Juglandaceae, it would be difficult to reconcile such an origin for the Fagales with a close relationship between the Fagales and the Hamamelidales, as has been implied by most modern classifications. He offered the alternate hypothesis that the Betulaceae and their closely related amentiferous allies may have converged on the Normapolles group in their pollen morphology. These patterns will become clearer only as additional paleobotanical evidence accumulates.

Although the family is old, it is neither particularly unspecialized nor greatly advanced. On the basis of wood anatomy, Hall found the Betulaceae to be moderately specialized relative to other woody angiosperm families. Sporne, in reviewing the degree of specialization of the flowers of a number of amentiferous taxa, found that for the Betulaceae 60 percent of the included characters could be considered primitive, compared with values of 88, 70, and 46 percent for the Magnoliaceae, Fagaceae, and Hamamelidaceae, respectively. Moseley, in a similar comparison but using both floral and vegetative characters, arrived at a figure of 43 percent for the Betulaceae, with values ranging from 27 (Ulmaceae) to 64 percent (Myricaceae).

The most obvious evolutionary trends within the Betulaceae are those related to fruit dispersal, as discussed above, and those correlated with apparent adaptations for survival in cold climates. The latter include shrubby growth forms, small leaves with few lateral veins, protection of the carpellate catkins during the winter by bud scales, and presence of true bud scales on the winter buds (Furlow, 1979; Jäger; Kikuzawa). These trends are identifiable in all of the genera of the family. Some of the related anatomical reductions involve retention of juvenile characteristics (Forsaith; Hall).

Members of the Betulaceae are economically important as timber trees, as the source of hazelnuts and filberts (*Corylus*), as ornamental trees and shrubs, and as an aid in soil nitrification and stabilization (*Alnus*). Some are important as causes of pollen allergies in regions where they grow abundantly (Dalen & Voorhorst; Lewis *et al.*; Løwenstein *et al.*; Solomon & Durham; Wodehouse, 1945). The bark of some contains substances of medicinal value (Lewis & Elvin-Lewis; Moerman). Wood of *Betula* and *Alnus* is widely used in the manufacture of furniture, paneling, boxes, and small wooden objects; that of *Carpinus* and *Ostrya* is used for making wooden tools such as mallets. In the past the bark of *Betula* has served as a commercial source of oil and methyl salicylate. The wood of several of the genera is used in the manufacture of high-quality charcoal.

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KEY TO THE SUBFAMILIES, TRIBES, AND GENERA OF BETULACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *monoecious, anemophilous, deciduous trees or shrubs; leaves simple, petiolate, pinnately veined, serrate or doubly serrate to subentire, ovate, elliptic, or obovate, alternately arranged, with deciduous stipules; staminate flowers reduced to (1–)4(–6) stamens and an equal number of tiny, scalelike tepals (or these absent), borne in scale-covered, pendulous catkins generally formed the growing season before anthesis; carpellate flowers usually consisting of a single inferior ovary composed of 2 (or 3) carpels, adnate to several tepals (when present), containing 2 locules below and 1 above, with 2 (or 3) linear stigmatic style branches, the ovules 2, parietal, borne near the summit, (except in* Corylus*) in usually uncrowded catkinlike, bracteate clusters; infructescences often strobiluslike, with large, conspicuous bracts; fruits 2-winged samaras, nutlets, or nuts.*

A. Staminate flowers with several scalelike tepals, carpellate flowers without a perianth; carpellate flowers 2 or 3 per bract in the inflorescence; ovules apparently unitegmic; infructescences 10–40 mm long, conelike, composed of many small, crowded, woody or coriaceous scales, each derived from several fused inflorescence bracts, these deciduous with the fruits or persistent; fruits small and laterally winged (the wings sometimes reduced to ridges) (subfamily Betuloideae).
  B. Stamens generally 4, entire; carpellate flowers 2 per bract; infructescence scales with (4 or) 5 lobes, greatly thickened, woody, and persistent long after release of the fruits. ..... 1. *Alnus.*
  B. Stamens 2, bifid below the anthers; carpellate flowers 3 per bract; infructescence scales with (1–)3 lobes, thickened but not woody, deciduous with the release of the fruits. ..... 2. *Betula.*

A. Staminate flowers lacking tepals, carpellate flowers bearing several scalelike tepals; carpellate flowers 2 per bract in the inflorescence; ovules bitegmic; infructescences larger, consisting of relatively uncrowded clusters with large subfoliaceous bracts, these deciduous with the fruits; fruits tiny to moderately large nuts, not winged (subfamily Coryloideae).
  C. Leaves narrowly ovate to elliptic, veins 10 or more; infructescences elongate, loosely arranged spikes of 3 or more pairs of leafy bracts, these each either subtending or enclosing a single nutlet (tribe Carpineae).
    D. Infructescence bracts flat, open, 1- to 3-lobed and variously toothed. ..... 3. *Carpinus.*
    D. Infructescence bracts forming inflated bladders, these completely enclosing the fruits. ..... 4. *Ostrya.*
  C. Leaves broadly ovate to suborbicular, veins 8 or fewer; infructescences irregular clusters of several small to moderately large nuts, these each surrounded by an involucre of several coarsely toothed leaflike bracts, the involucre sometimes long and tubular (tribe Coryleae). ..... 5. *Corylus.*

Subfamily BETULOIDEAE

Tribe BETULEAE

1. **Alnus** Miller, Gard. Dict. abr. ed. 4. [alph. ord.] 1754.

Small to large shrubs [or small to medium-sized pyramidal to round-crowned trees], usually with several trunks; branching excurrent to deliquescent, when

excurrent, often becoming deliquescent in age; trunks and branches terete, the branchlets and twigs subdistichous to diffuse; twigs sometimes differentiated into pronounced long and short shoots (subg. ALNOBETULA). Bark close, thin and smooth [to thick, furrowed, and corky], when smooth usually dark and marked with prominent pale lenticels, these sometimes becoming elongate horizontally; young twigs glabrous or sparingly pubescent, often covered with resinous glands; leaf scars triangular to crescent shaped, with 3 more or less equidistant, deeply crescent-shaped vascular bundle scars; winter buds long stalked or subsessile, narrowly to broadly ovoid or elliptic, terete, often held more or less parallel to the twig, the apex acute to rounded, with 2 valvate (stipular) or several imbricate scales [or sometimes naked]; wood fine grained, nearly white, turning reddish upon exposure to air, moderately soft, moderately light in weight; pith triangular in cross section. Leaves 3-ranked to subdistichous, borne on long [or short] shoots; blades thin [to very leathery], ovate to elliptic or obovate, doubly serrate, serrate, serrulate [or subentire], abaxially glabrous to tomentose, sometimes covered abaxially with resinous glands; secondary venation craspedodromous [or semicraspedodromous], mostly divergent and straight; leaves open and convex in bud, becoming conduplicate and plicate upon expansion; stipules broadly ovate [to narrowly linear]. Staminate catkins terminal [or lateral in leaf axils near the ends of branchlets], [solitary or] in racemose clusters, formed during the previous growing season and exposed [or enclosed in buds] during the winter, expanding before or with the leaves [or (in subg. CLETHROPSIS) formed and expanding during the same growing season], crowded, the scales ovate, consisting of 5 fused bracts; carpellate catkins lateral, below the staminate, either on short shoots or laterally in leaf axils on long shoots, [solitary or] in small [to large] racemose clusters, developing and maturing at the same time as the staminate, exposed or enclosed within buds during the winter, short, ovoid to ellipsoid, firm and erect to subpendulous, crowded, the scales composed of 5 fused bracts. Staminate flowers 3 per scale in the catkins, each with (3 or) 4(–6) scalelike tepals and an equal number of stamens, these borne opposite the tepals, undivided; pollen grains flattened, 19–27 μm in diameter, strongly aspidote, with (3 or) 4 or 5 (or 6) elliptic equatorial apertures connected by conspicuous pairs of thickened bands (arci). Carpellate flowers sessile, normally 2 per scale, rarely with 1 or more staminodes or vestigial tepals (the latter, when present, adnate to the ovary); ovule 1 by abortion, unitegmic. Infructescences ellipsoid, ovoid [or short-cylindrical], strobiloid, conelike, borne [singly or] in racemose clusters, erect and subsessile or pendulous on long, thin peduncles, the bracts connate into woody, 5-lobed scales, these persistent until after dispersal of the fruits. Fruits small, ellipsoid to ovoid, rostrate samaras, maturing and dispersed the same season as [or the season following] pollination, the styles persistent, the wings 2, lateral, membranaceous, reduced in some species, the pericarp thin. Seeds with membranaceous testa and flat cotyledons; germination epigeal. Chromosome numbers $2n = 14, 28, 42, 56$. LECTOTYPE SPECIES: *Alnus glutinosa* (L.) Gaertner; see Furlow, Rhodora **81:** 74. 1979. (The ancient Latin name for the alder, used by Virgil, Pliny, and others; derived from *alo,* to nourish, in reference to its usual close association with water.)—ALDER.

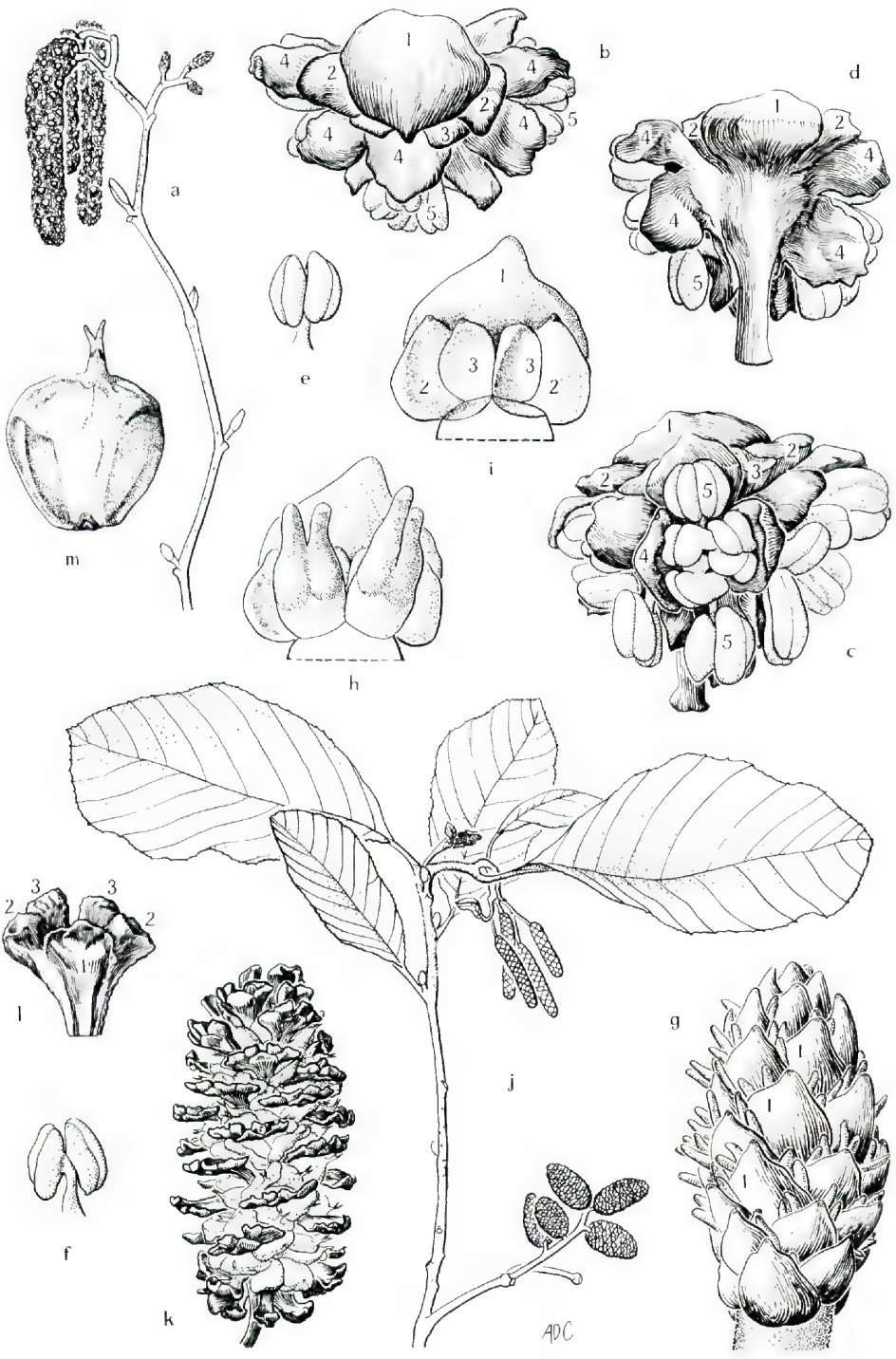

FIGURE 1. **Alnus.** a–m, *A. serrulata*: a, flowering branchlet, pendent staminate catkins at upper left, carpellate catkins at upper right, ×½; b, flowering staminate cymule oriented as on catkin in "a," primary, secondary, and tertiary bracts (1, 2, 3) visible along with tepals of 3 flowers (4) and tips of anthers of 2 of these (5), ×8; c, staminate cymules of

About 25 species of forested parts of the temperate and boreal Northern Hemisphere and Central America south to northern Argentina at high elevations. The alders resemble the birches but are easily distinguished from them by their infructescences, which consist of persistent woody scales with five lobes (vs. thin, deciduous, three-lobed scales). Except in members of subg. ALNOBETULA (which have subsessile buds with several true scales), they are also distinctive in having stipitate buds with two stipular scales. The fruits, borne two to a scale, are laterally winged, although the wings are sometimes reduced (occasionally to mere ridges).

The alders have been variously combined and split at the generic level by many authors. Linnaeus and his immediate followers combined *Alnus,* as used by Tournefort and Linnaeus himself in the first edition of *Genera Plantarum,* with *Betula,* while Czerepanov, Ledebour, Murai (1963), Spach (1841), and others have treated the present subgenera as genera. However, historically and currently the genus has most widely been held to constitute a single natural entity. In addition to the family monographs, taxonomic work in *Alnus* has included a series of descriptive papers by Callier (1892, 1911, 1918), synopses by Czerepanov and Murai (1964), and a revision of the American taxa by Furlow (1979).

The genus is diverse, including four distinct lines of specialization. These are sometimes given generic status but are here treated as subgenera (ALNUS, ALNOBETULA, CLETHROPSIS (Spach) Endl., and CREMASTOGYNE Schneider in Sarg.). Subgenera ALNUS and ALNOBETULA are further divided into sections, detailed below. Seven native (and several naturalized) species representing three of the four subgenera occur in North America north of Mexico, with an additional two being distributed throughout the mountains of Mexico, Central America, and northern South America (Furlow, 1979). Species of subg. CREMASTOGYNE, characterized by stipitate two-scaled buds, solitary axillary staminate and carpellate catkins, long-pedunculate infructescences, and fruits with broad hyaline wings, are restricted to south-central Asia.

Subgenus ALNUS is characterized by a shrubby or arborescent habit, winter buds with long stalks and two valvate (stipular) scales, inflorescences borne in racemose clusters, and development of both carpellate and staminate inflorescences (which are exposed during the winter) during the growing season prior to anthesis. Its most unspecialized segment (sect. PHYLLOTHYRSUS Spach) con-

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3 flowers, adaxial view, central flower seen from above, its 4 tepals (4) and 4 stamens (5) visible, bracts at top of illustration as in "b" (1, 2, 3), ×8; d, staminate cymule, abaxial surface, 2 lateral flowers seen from side, tepals (4) and stamens (5) partly visible, bracts as in "b" and "c," ×8; e, f, stamens, showing short filaments and partial division of anthers, ×8; g, carpellate catkin at anthesis, each scale subtending 2 flowers, only primary bracts (1) and paired stigmas visible, ×10; h, adaxial view of carpellate cymule with 2 flowers (ovaries undeveloped), bracts partially visible, ×20; i, scale with flowers removed to show primary, secondary, and tertiary bracts (1, 2, 3), ×20; j, late-season branchlet with mature infructescences and next season's carpellate catkins above and staminate ones pendent, ×½; k, infructescence with mature fruits (stippled), ×3; l, mature infructescence scale, abaxial surface, showing 5 lobes derived from primary, secondary, and tertiary bracts (1, 2, 3), ×6; m, mature fruit, style remnants at summit, ×8.

sists of large trees of western North America, Mexico, and Central America (*Alnus acuminata* HBK., *A. jorullensis* HBK., *A. oblongifolia* Nutt., and *A. rubra* Bong.), while sect. ALNUS (subg. *Gymnothyrsus* (Spach) Regel; sect. CLETHRA W. D. Koch) includes shrubby, more northern forms. In the United States and Canada sect. ALNUS is represented by four taxa. *Alnus incana* (L.) Moench subsp. *rugosa* (Du Roi) Clausen and subsp. *tenuifolia* (Nutt.) Breitung, large shrubs of riverbanks and marshy areas, occur throughout the cooler portion of the Temperate Zone across the continent. In the East subsp. *rugosa,* speckled or tag alder, characterized by dark, lenticel-speckled bark and ovate to elliptic, coarsely doubly serrate leaves, is more or less confined to the region north of the glacial boundary. Subspecies *tenuifolia,* thinleaf or white alder, distinctive in its lighter bark and smaller leaves with more evenly spaced and less acute teeth, is distributed across much of northwestern Canada and through the western mountains as far south as central California and New Mexico. Additional subspecies occur at equivalent latitudes in Europe and Asia. *Alnus serrulata* (Aiton) Willd., smooth alder, occurs throughout the Atlantic and Gulf coastal plains, in the southern Appalachians and the Ozark Highlands, and northward in the Mississippi Embayment. Its leaves are large, somewhat leathery, elliptic to obovate, and serrulate or finely and irregularly doubly serrate. The distribution of this species is essentially coastal, but it reaches north to central Ohio and Indiana in the interior, and to New York and Massachusetts in the East. Disjunct populations occur along the St. Lawrence River and the lower Great Lakes to southern Lake Michigan. The remaining species, *A. rhombifolia* Nutt., white alder, is a small tree of riverbanks and canyons in mountains of the western United States.

Subgenus ALNOBETULA consists of shrubby species of regions with cold climates. It has sometimes been segregated as a separate genus, *Alnaster* Spach (*Alnobetula* Schur, *Semidopsis* Zumaglini, *Duschekia* Opiz; see Furlow, 1979). In this group the buds are subsessile and covered by several imbricate scales. Both staminate and carpellate catkins are formed the season before anthesis, but only the staminate ones are exposed during the winter. In North America it is represented by the circumpolar *Alnus viridis* (Chaix) DC. in Lam. & DC. In the Northeast the transcontinental, far-northern subsp. *crispa* (Aiton) Turrill, green alder, occurs along the Appalachian Mountains at progressively higher elevations southward to central New York and Massachusetts, with disjunct populations in southern Pennsylvania (Wherry) and on the summit of Roan Mountain on the Tennessee–North Carolina border (Brown; Clarkson; A. Gray, 1842). It grows along streambanks and also in rocky and drier sites in colder climates. This subspecies is recognizable by its medium-sized, ovate, serrulate or finely serrate, usually glutinous leaves and its subsessile buds with more than two scales.

In western Canada, and southward in the mountains of the Northwest, subsp. *crispa* is replaced by subsp. *sinuata* (Regel) Löve & Löve, Sitka alder, a large shrub with larger, broader, thinner, more coarsely toothed leaves. This subspecies occurs along streams and frequently covers moist mountain slopes near the timberline, especially where landslides have created open areas. Subspecies *fruticosa* (Rupr.) Nyman is distributed from coastal Alaska to British Columbia,

Washington, Oregon, and northern California, as well as across the Bering Strait in northeastern Asia (Furlow, 1983b). Its vegetative morphology somewhat resembles that of subsp. *crispa,* with which it has sometimes been confused in the past. Subspecies *viridis* is distributed throughout the mountains of western Europe.

The predominantly Asian subg. CLETHROPSIS is represented in America by a single species, *Alnus maritima* Muhl. ex Nutt., a small tree of stream banks, marshes, and the shores of shallow lakes. Its distribution is limited to two widely disjunct populations, one on the Delaware-Maryland-Virginia peninsula and the other in south-central Oklahoma (Furlow, 1979; Stibolt). Members of subg. CLETHROPSIS are unique in that they bloom in autumn, rather than in spring. They also differ from other native species in having essentially naked buds, leaves with semicraspedodromous venation, and solitary carpellate inflorescences borne in the axils of foliage leaves. This group was considered to be the most primitive one in *Alnus* by Murai (1963) and Takhtajan (1969) on the bases of morphology and phytogeography. However, Furlow (1979) concluded that many of its distinctive structural and life-history features represent derived conditions, and he placed it in a moderately advanced position in the family. Van Steenis, following Regel, has treated populations of the Asian *A. japonica* (Thunb.) Steudel as conspecific with American *A. maritima.* However, no critical comparison of the two has been made to determine the soundness of that arrangement.

Alnus serrulata, a common shrub along open streambanks throughout the region, was erroneously called *A. rugosa* by Britton & Brown (1896, 1913), Robinson & Fernald, and Small (1903, 1933) (see also Fernald, 1945a), and misapplication of the name *A. rugosa* continues in a few floras and herbaria. *Alnus incana* subsp. *rugosa,* a related taxon reaching its southern limit in West Virginia in the mountains and in Maryland on the Coastal Plain, hybridizes with *A. serrulata* where their ranges overlap, and extensive and often unrecognized hybrid swarms are formed (Furlow, 1979; Steele). From the results of a serological study (based on limited material taken entirely from the region of geographic overlap), Villamil & Fairbrothers concluded that the two taxa constitute a single species. Woodworth (1929a, 1930a) described apomixis from populations of *A. serrulata* (which he called *A. rugosa*) taken from this swarm. However, in a later paper (1931), he showed that populations located away from the region of intergradation have normal cytological characteristics. The two species are not difficult to distinguish in the field outside the region of overlap. *Alnus serrulata* has elliptic to obovate leaves, often with rounded apices and with very small teeth, while *A. incana* subsp. *rugosa* has ovate to elliptic leaves with acute apices and usually coarse, doubly serrate margins. The species are also distinguishable by the dark, rather shiny red-brown bark marked by prominent light-colored lenticels in *A. incana* and the dull, uniform light gray or light brown-gray bark with inconspicuous lenticels in *A. serrulata.*

The least-well-understood segments of the genus, with respect to the diversification and relationships of the genus as a whole and to the circumscription of individual species and infrageneric groups, are those occurring in Latin America and China. The Latin American species, all members of subg. ALNUS

sect. PHYLLOTHYRSUS, were mostly described by Bartlett and Fernald (1904a), who were later followed by Standley. Furlow's (1977, 1979) study of this complex showed the many species and varieties to constitute two species consisting of a number of somewhat incompletely differentiated geographic and ecological races. He concluded that this group demonstrated many of the most unspecialized characters in the genus and represented remnants of a very old introduction from Asia, possibly dating from the Miocene or earlier. The relationships of the Asian taxa, particularly of species of subgenera CLETHROPSIS and CREMASTOGYNE, to the better-known American and European species, have not been taken sufficiently into account by Western taxonomists. These species will need to be studied thoroughly before many questions regarding the origin and diversification of the genus can be answered.

The shrubby habit of the northern and eastern North American alders is regarded as a specialized condition that evolved in response to harsh northern winters. The species of more equable regions (e.g., the Pacific Northwest, the mountains of Latin America, and the foothills of the Himalayas) become large trees and develop relatively thick, corky bark. It has been shown by both Forsaith and Hall that some shrubby species of *Alnus* retain juvenile wood characters, suggesting that the shrub habit was derived through neoteny. The existence of the shrub habit in several divergent lines within the genus suggests that it has arisen independently several times.

Leaves of species other than those in subg. CLETHROPSIS are rather uniform in morphology, varying mostly in size, general shape, and size of the serrations. Occasionally forms with deeply cut leaves occur naturally (see Hylander, 1957a), and these have attracted horticultural interest. In leaf venation and margins species of subg. CLETHROPSIS differ both from other *Alnus* subgroups and from other Fagales. The teeth are small, distant, and single (although on the basis of secondary vein endings, they are apparently derived from a doubly serrate form). The secondary veins branch before reaching the tooth: one of the branches enters the tooth along its apical edge, and the other connects with another vein or ends in the adjacent tooth. The tertiary (cross) veins are poorly developed in relation to those in other species.

The leaves of *Alnus,* like those of the other Betulaceae, bear trichomes of various types, including simple hairs, which are sometimes extremely dense on the abaxial surface, as well as both stipitate and sessile glands (Furlow, 1979; Hardin & Bell). In some taxa (e.g., *A. jorullensis* subsp. *lutea* Furlow and *A. viridis* subsp. *crispa*) these glands are large and conspicuous under magnification and have been given diagnostic status (e.g., by Standley). However, the great variability in the presence and prominence of the glands, like the variation in leaf pubescence, renders their use for identification largely ineffective (Furlow, 1979).

The wood anatomy of *Alnus* is the least specialized in the family (Hall). It is similar to that of *Betula* (e.g., some species have opposite intervascular pitting, perforation plates with many scalariform bars, and vessels usually frequent and small (Furlow, 1979; Hall)), although certain species are characterized by more advanced features. *Alnus viridis* appears to be the most specialized of the American species, while *A. incana* and *A. serrulata* are of

intermediate advancement (Furlow, 1979) and *A. maritima* contains a mixture of primitive and advanced features.

The structure of the flowers and inflorescences of *Alnus,* together with their various adaptive trends, have been elucidated by Abbe (1935, 1938) and Hjelmqvist (1948). The staminate catkins consist of helically arranged cymules of three sessile flowers. Subtending each cluster are one primary, two secondary, and (usually) two tertiary bracts. Each flower consists of from (one to) four to six tepals and stamens (usually four in subg. ALNUS), with the stamens opposite and adnate to the tepals at the base. Where six tepals are present, these are borne in two whorls of three (Abbe, 1935). The thecae are connate or slightly separated by a short, forked connective. The short carpellate catkins consist of extremely crowded cymules of two flowers (apparently reduced from three, as seen in *Betula*) and are subtended by a scale made up of the same five bracts that subtend the staminate cymules. The ovaries were characterized as "nude" (apparently inferior on the basis of vascular traces, but lacking a perianth) by Abbe (1935). The staminate inflorescences are comparable to those of *Betula,* except that the tertiary bracts have been retained. In comparison to *Betula,* the carpellate cymules are specialized in having lost the secondary (central) flower, but primitive in having retained their tertiary bracts.

A simple progression of forms in the genus leads from racemose clusters of catkins (the carpellate borne below the staminate) to solitary axillary catkins by reduction (Furlow, 1979; Jäger; Hjelmqvist, 1948; Murai, 1964). In subgenera ALNUS and ALNOBETULA the staminate and carpellate catkins occur in separate clusters on different shoots; however, the carpellate catkins are produced on new growth in the spring in subg. ALNOBETULA, while they are formed the season before anthesis in subg. ALNUS. *Alnus maritima* has clustered staminate and solitary carpellate catkins (occurring on the same shoot). Murai (1963) viewed this condition as primitive; however, Furlow (1979) argued that the solitary carpellate inflorescences of subg. CLETHROPSIS are most likely of secondary origin by reduction of flowering branch systems such as those seen in subg. ALNUS.

The genus has been studied cytologically by Gram and colleagues, Jaretzky, Poucques, Wetzel (1927, 1928, 1929), and Woodworth (1929a, c; 1930a). All of the American species for which data are available have chromosome numbers of $2n = 28$. Other members of the genus form a polyploid series of $2n = 14$, 28, and 56, with several counts of $2n = 42$, these apparently having originated through hybridization between $2n = 28$ and $2n = 56$ types (see Furlow, 1979). The base chromosome number of *Alnus* ($x = 7$) is based on a single report (Chiba), but this is also supported indirectly by other cytological evidence (Brown & Al-Dawoodie) and the results of allozyme studies (Bousquet *et al.,* 1987a, 1988), which show plants with $2n = 28$ to behave genetically as tetraploids.

The alders are anemophilous and produce abundant pollen at anthesis (Wodehouse, 1935), which in temperate North America occurs before (subg. ALNUS) or at the same time as (subg. ALNOBETULA) the unfolding of new leaves, or in late summer (subg. CLETHROPSIS) just after the new catkins mature. The latter condition has been interpreted as precocious and therefore derived (Fur-

low, 1979). In Latin American populations (subg. ALNUS sect. PHYLLOTHYRSUS) anthesis occurs mostly in December and January (very early spring). The shrubby northern species often form extensive thickets that give the impression of clonal growth. However, genotypes in such populations have been found to be randomly distributed in *Alnus incana* subsp. *rugosa* (Huenneke), suggesting that they result from seeding, rather than from vegetative reproduction. In all species the tiny fruits are abundantly produced and widely distributed. In some species, as in *Betula,* the fruits are winged and are carried by the wind. In others (e.g., *A. serrulata*) the wings have been reduced to ridges, in which case dispersal may be primarily by water currents. Allozyme studies by Bousquet and colleagues (1987a–c, 1988) have shown low inbreeding with high levels of gene flow within populations of both *A. incana* subsp. *rugosa* and *A. viridis* subsp. *crispa.* Little population differentiation was noted in these studies (1987b, 1988), suggesting relatively high interpopulational gene flow as well. Members of the genus hybridize readily where species occur together. However, most species are separated by habitat or geography, and except at the intersections of the ranges of the various taxa, extensive genetic mixing does not occur. Lists of named hybrid taxa in the genus are provided by Murai (1964) and Winkler.

Alnus (and *Betula*) appear earlier in the fossil record than the other Betulaceae (Crane & Stockey; L. J. Hickey & Doyle; Wolfe, 1973), but the precise time and place of origin of the genus, like those of the family, are a matter of speculation. Takhtajan (1969) believed that the group developed in southwestern Asia, while Murai (1964) placed its origin in the area of present-day Japan. Furlow (1979) concluded that the alders most likely originated in temperate Asia, with diversification there followed by progressive migrations east and west into Europe and the New World. The species of *Alnus* currently inhabiting North America appear, from fossil and phytogeographic evidence, to have entered from both the east and the west at several different times (Furlow, 1979; McKenna; cf. Löve & Löve). The ancestors of both *A. maritima* and the Latin American taxa may have entered in the early Tertiary from Asia. Using fossil pollen, Graham (1973a) concluded that *Alnus* and other woody mesophytic genera from northwestern North America migrated to southern Latin America during the Miocene. Graham (1973a) and Martin & Harrell have reviewed the evidence covering the introduction of this element into southern Mexico and Central America (cf. Deevey; Dressler; Miranda & Sharp).

Fossils suggest that subgenera ALNUS and ALNOBETULA had already differentiated and were present in western North America by the Miocene (Wolfe, 1969). However, a recent study employing allozyme data (Bousquet *et al.,* 1988) placed the time of divergence of *Alnus incana* subsp. *rugosa* from *A. viridis* subsp. *crispa* populations at only about one million years ago. The American subspecies of *Alnus viridis* and (to a lesser extent) *A. incana* are only very slightly differentiated morphologically from their Eurasian races, and it seems likely that they may be of recent (possibly post-Pleistocene) introduction, especially in the West (cf. Hultén). However, as noted by Bousquet and colleagues (1988), Furlow (1979), and others, it is possible that these species, at least in part, survived Pleistocene glaciations in refugia in northern North America. *Alnus serrulata,* closely related to *A. incana* on the basis of mor-

phology (Furlow, 1979), may have entered from Europe at an earlier time. However, alder pollen is not known in the pre-Pleistocene sediments of the Atlantic and Gulf coastal plains where *A. serrulata* would be expected to have existed during the Pleistocene (J. Gray).

The alders associate symbiotically with species of the actinomycete *Frankia,* which lead to the formation of nodules on the roots of the plants and fix atmospheric nitrogen (Bond; Bond *et al.*; Dalton & Naylor; Hawker & Fraymouth). The importance of alders in plant succession is well documented for different species and a variety of physical settings (e.g., Crocker & Major; Fremstad; Newton *et al.*; Reiners *et al.*; Tarrant, 1968; Ugolini). During the past two decades foresters and plant physiologists have shown great interest in the nitrogen-fixing ability of actinorhizal plants, and an extensive literature has developed related to research into details of the process and the biology of the organisms involved, including identification, isolation, cultivation, morphogenesis, ultrastructure, ecology, nitrogen-fixing activity, inheritance, metabolism, chemosystematics, growth, reaction to various environmental factors, nutritional requirements, infection of hosts, and host-endophyte interactions. Some of this work represents biotechnological research aimed at the "genetic improvement" of alders and their symbionts (see Gordon *et al.*; Hall & Maynard; Hall, McNabb, Maynard, & Green; Hall, Miller, Robison, & Onokpise; Normand & Lalonde). Of special interest is the genetic recombination of large tree species, especially *Alnus glutinosa,* European black alder, *A. rubra,* red alder, *A. cordata* (Loisel.) Loisel., Italian alder, *A. incana* (L.) Moench subsp. *incana,* European white alder, and other species. This activity is in part due to a recent interest in the possible use of alders in intensive silviculture (see Dickman; Gordon & Dawson; Tarrant, 1983). Symposium papers dealing with this subject have been published by Gordon & Wheeler, Gordon, Wheeler, & Perry, and Torrey & Tjepkema (1979, 1983). The articles cited illustrate the range and scope of current work in this field.

Alders are not seriously bothered by diseases or insect pests, although various insects feed on their foliage (Sargent, 1896). In the Southeast cottony scale insects are frequent parasites of *Alnus serrulata.* Hepting reviewed the many fungal diseases known to affect *Alnus,* but he concluded that most are of little or no economic importance. The most serious pathogen of tree-sized alders in North America is heart rot (*Fomes ignarius* (L.) Kickx), which usually appears only in trees over 40 years old (Hepting; Worthington *et al.*). A species of *Taphrina* affects the carpellate catkins of many species, resulting in curled, straplike enlargements of the infructescence bracts.

The shrubby species of *Alnus* in eastern North America are mostly opportunistic plants that rapidly colonize disturbed habitats. In other parts of the world, the genus includes large trees that are important components of the mature natural vegetation. In the Pacific Northwest *A. rubra* is a dominant tree of floodplain forests, where it has considerable commercial value. Throughout the mountains of Mexico and Central America, *A. acuminata* and *A. jorullensis* become large trees and serve locally as a source of lumber.

Alders have been put to a great many uses by many cultures throughout the centuries. Various groups of North American Indians, as well as white settlers

in the New World, utilized the astringent properties of alder bark for a wide variety of medicinal purposes, including the treatment of burns, infections, leukorrhea, toothaches, and indigestion (see Lewis & Elvin-Lewis; Moerman). The triterpenes betulin and lupeol, extracted from bark and wood of *Alnus rubra,* have recently been found to have antitumor activity in laboratory animals (Sheth *et al.*). In regions where alders make up a significant part of the vegetation, their pollen is an important cause of hay-fever allergies (Chamberlain, 1927; Florvaag & Elsayed; Florvaag, Elsayed, & Apold; Florvaag, Elsayed, & Hammer; Lewis *et al.*; Løwenstein *et al.*; Solomon & Durham). In Europe and America the wood, which is fine grained, although rather soft and not very durable, has been used for beams and piles, shipbuilding, cabinetry, boxes, and the manufacture of a wide variety of small wooden objects, ranging from toys and tool handles to wooden shoes. The wood was formerly greatly valued for the production of high-quality charcoal for gunpowder manufacture. One of the most important present uses in the United States and Canada, especially in the Pacific Northwest, is as a source of pulpwood for making paper (Worthington *et al.*). The U. S. Forest Service has published two symposium volumes (Briggs *et al.*; Trappe *et al.*) dealing with aspects of alder taxonomy, ecology, and silviculture, with particular reference to *A. rubra.* Several species, especially the European *Alnus glutinosa, A. incana* subsp. *incana,* and *A. cordata* in the East and *A. rubra* in the Northwest, are occasionally cultivated as ornamentals.

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2. **Betula** Linnaeus, Sp. Pl. **2:** 982. 1753; Gen. Pl. ed. 5. 422. 1754.

Small to large, conical, pyramidal, or round-crowned trees [or small to large shrubs], often with several trunks; branching excurrent (becoming deliquescent in age) [or in shrubby forms mostly excurrent]; trunks and branches terete, the branchlets and twigs subdistichous; twigs usually differentiated into pronounced long and short shoots. Bark thin and smooth, dark brown to chalky white, often exfoliating in very thin layers, becoming thicker and scaly or furrowed in age, marked with prominent lenticels, these frequently becoming much elongated horizontally; young twigs glabrous or sparingly pubescent, often covered with resinous glands, sometimes aromatic when crushed; leaf scars crescent shaped to suboval, with 3 nearly equidistant circular to elliptic vascular bundle scars; winter buds sessile, slender, terete, divergent or appressed along the lower half, the apices acute, with several smooth imbricate scales, only the outer 3 generally visible; wood fine grained, nearly white to reddish brown, moderately hard, moderately heavy; pith circular or remotely triangular in cross section. Leaves subdistichous, usually borne on short shoots; blades thin, ovate to deltoid, elliptic [or suborbicular], doubly serrate [or serrate to shallowly lobed], glabrous to abaxially tomentose, sometimes covered abaxially with resinous glands; secondary venation craspedodromous, the veins mostly divergent and straight; leaves in bud open and convex, becoming conduplicate and plicate during expansion; stipules broadly ovate. Staminate catkins terminal [or lateral in leaf axils near the ends of branchlets], [solitary or] in small racemose clusters, formed the previous growing season and exposed [or enclosed in buds] during the winter, expanding with the leaves, densely arranged, the scales ovate, consisting of 3 fused bracts; carpellate catkins lateral on the branchlets, below the staminate, mostly borne on short shoots, usually solitary, developing at the same time as the staminate, enclosed within buds during the winter and expanding with the leaves, ovoid to cylindrical, firm and erect, scales and flowers crowded, the scales compact, consisting of 3 fused bracts. Staminate flowers 3 per scale in the catkin, consisting of [(1 or)] 2–4 scalelike tepals and [(1 or)] 2 or 3 [(or 4)] stamens, these divided nearly to the base (giving the impression of twice as many stamens with 1-locular anthers); pollen grains flattened, 15–30(–40) μm in diameter, with 3(–7) elliptic equatorial apertures. Carpellate flowers sessile, [(1–)]3 per scale, consisting of a single 2-locular

ovary with 2 linear styles, sometimes with 1 or more staminodes; ovule 1 by abortion, unitegmic. Infructescences cylindrical to ovoid, strobiluslike, erect or pendulous on short peduncles, the bracts connate into coriaceous or somewhat woody [(1- or)] 3-lobed scales, these usually readily deciduous with the fruits. Fruits small, ellipsoid to ovoid, rostrate samaras, maturing and dispersed the same season as pollination, styles persistent, the wings lateral, membranaceous, the pericarp thin. Seeds with membranaceous testa and flat cotyledons; germination epigeal. Chromosome numbers $2n = 28, 42, 56, 70, 84$. LECTOTYPE SPECIES: *Betula alba* L.; see N. L. Britton, N. Am. Trees, 246. 1908. (The Latin name for birch used by Pliny; from *batuere,* "to beat," for the birch rods used by Roman lictors to beat back crowds of people.)—BIRCH.

About 35 species of small to large trees and shrubs of the Temperate and Boreal zones of the Northern Hemisphere. Like *Alnus,* the genus is highly diversified, especially in the Old World. In the United States and Canada it includes about 17 species, which occur in the area south to the Gulf Coastal Plain in the East and to Colorado and central California in the mountains of the West. The species hybridize freely; 16 named hybrids are listed by Kartesz & Kartesz. The birches occupy a variety of habitats, characteristically including peat lands; stream banks; lake shores; cool, damp woods; cool, moist slopes in coves; and (in cooler regions) drier, more open sites.

Spach (1841) treated the birches as two genera, *Betula* and *Betulaster,* the latter an Asian group distinguished by many-veined, acuminate-toothed leaves, fruits with exceptionally wide wings, and carpellate inflorescences (and fruiting catkins) borne in racemose clusters. In his monograph of the Betulaceae, Regel (1861) recognized these two major groups as parts of *Betula* but did not clearly denote their rank or names. He indicated that these were subgenera in his subsequent (1865) revision of *Betula* and *Alnus,* but he again failed to provide a suitable name (erroneously referring to Spach's genus *Alnaster,* a segregate of *Alnus*). In his revision for De Candolle's *Prodromus,* Regel (1868) named these taxa properly at the rank of section. In his 1865 revision, he further divided the two major groups into seven taxa bearing only the rank of "Gruppe." Winkler (1904) treated the two major taxa as sections of *Betula,* subdividing these into four subsections corresponding to various of Regel's subgroups, and W. D. J. Koch, Koehne, Schneider, and others have since elevated most of them to sections, the arrangement adopted by Kuzeneva and the one used here.[3] Endlicher (1842, 1847) is frequently cited as the author of sections or subgenera in *Betula,* but he did not indicate ranks for his names either in the text or in his subsequent references to it (see Brizicky). In a recent synopsis of the genus, Fontaine recognized 52 species, 24 varieties, eight natural hybrid species, and 23 cultivars and artificial hybrids.

Section COSTATAE (Regel) Koehne consists of large, mesophytic trees, often with dark (close or exfoliating) bark; large, thin leaves; infructescence scales

[3]Sections COSTATAE (Regel) Koehne and HUMILES W. D. Koch have not yet been treated at the subgeneric level—perhaps a better course, considering their high degree of differentiation (equivalent to that of the subgenera of *Alnus*).

FIGURE 2. **Betula.** a–j, *B. nigra*: a, flowering branchlet with 2 ascending carpellate catkins and 3 pendent staminate ones, ×½; b, staminate cymule, oblique view of adaxial side, showing stamens of 3 flowers (tepals not visible) and tips of primary and secondary bracts (1, 2), portion of axis of catkin below, ×8; c, same, side view, primary and secondary bracts at left, ×8; d, staminate cymule, seen as in "b," anthers removed, to show primary (1) and secondary bracts (2), 1 tepal (4) of each of 3 flowers, and partial filaments of each of 6 stamens, ×8; e, 2 views of stamens, showing half-anthers, ×12;

with long, narrow lobes; and fruits with relatively narrow wings. Three species of this group occur in the southeastern United States. *Betula nigra* L., river birch, red birch, a large (to 30 m) tree usually with spreading clusters of trunks (each up to 1 m in diameter), distinctive rhombic-ovate leaves, and creamish to reddish exfoliating bark on young branches (dark, scaly bark on older trunks), is found throughout the region, except in peninsular Florida and certain areas of the Gulf Coastal Plain, including Alabama, Mississippi, Louisiana, and Arkansas (see Coyle *et al.*, 1983b; Duncan; Koevenig). This species grows on stream banks and on bottomlands. Cribben & Ungar, Fritts & Kirtland, and McClelland & Ungar have shown that in Illinois and Ohio river birch is predictably present on acid soils, especially along streams heavily affected by coalmine drainage, and largely absent from alkaline soils. However, Wolfe & Pittillo found no such relationship in western North Carolina and concluded that in their area, the availability of continuous moisture constituted the most important limiting factor. *Betula nigra* is unique among our species in that its fruits mature, are released, and germinate in early summer, apparently an adaptation associated with the floodplain habitat (which is frequently inundated in the spring). *Betula alleghaniensis* Britton, yellow birch, and *B. lenta* L., cherry birch, sweet birch, black birch, are more northern, occurring in suitable habitats from southern Newfoundland to southeastern Manitoba and southward along the Appalachians to northern Georgia and northern Alabama (*B. lenta* only). *Betula alleghaniensis* (incorrectly spelled "*alleghanensis*" by Britton & Brown, 1913) is a large forest tree, usually with a single trunk, reaching a height of about 35 m and a trunk diameter of 1.5 m. Its leaves are large, thin, ovate, and doubly serrate. The bark of young branches is usually yellowish and exfoliates in ragged curls, but Dancik and Dancik & Barnes (1971) have shown this character to be inconsistent. The bark of older trunks becomes dark and scaly. *Betula lenta* has somewhat similar characteristics, but it is smaller and its dark cherrylike bark does not exfoliate. The two species can be distinguished by their infructescence scales, which in *Betula alleghaniensis* have pubescent, more elongate, and often more strongly ascending lateral lobes and in *B. lenta* glabrous, more expanded, more divergent ones. The bark and twigs of both species contain wintergreen oil (methyl salicylate), which can be detected by chewing fresh twigs. *Betula alleghaniensis* is an important constituent of the hemlock-hardwoods forest in the northern Appalachians, occurring on a variety of soil types and in various drainage conditions. In the southern Appalachians it occurs only at elevations over 1000 m. The yellow birch has been widely known in the past as *B. lutea* Michx. f., a superfluous and therefore illegitimate name (Michaux, after first misapplying the name *B. excelsa* to the

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f, adaxial side of carpellate cymule of 3 naked flowers, tips of primary and secondary bracts visible, ×8; g, bract complex, abaxial side, the 2 secondary bracts (2) partially united with the primary one (1), style tips of cymule visible, ×8; h, branchlet with mature infructescences, ×½; i, abaxial side of 3-lobed bract complex of mature carpellate cymule (primary bract and 2 secondary bracts partially united (see g), ×6; j, mature achene with membranaceous lateral wings, ×6. k, l, *B. lenta*: k, branchlet with mature infructescences, ×½; l, abaxial side of bract complex of mature fruiting cymule (cf. g, i), ×6.

yellow birch, substituted the epithet *lutea,* which he considered more descriptive; see Brayshaw, 1966a).

Betula uber (Ashe) Fern., known for many years only from herbarium material (Mazzeo), was rediscovered in 1975 in a single southwestern Virginia population (Ogle & Mazzeo; Reed). On the basis of leaf shape, the presence of wintergreen oil in its bark, and other characters, it had been speculated that this birch could represent a relative or hybrid of *B. pumila* L. (now occurring 500 miles to the north) or a variant or hybrid of *B. lenta* (see A. G. Johnson). However, wood anatomy clearly places *B. uber* in sect. COSTATAE, not with the dwarf birches, and additional evidence suggests that it is not closely related to other sympatric species of that section (e.g., *B. lenta*) (Hayden & Hayden). This view is supported by discriminant analysis (Sharik & Ford).

The mostly circumboreal sect. BETULA (sect. *Albae* (Regel) Schneider) consists of small to medium-sized trees with rather large, thin leaves and fruits with relatively wide wings (wider than the body of the fruit). A characteristic feature of trees in this group is their white bark, which often peels apart in sheets due to its alternating layers of tabular cells with thick walls and larger ones with thin walls, the latter containing grains composed largely of the triterpenoid betulin, which also makes the bark waterproof (Metcalfe & Chalk). The birches of northern North America with white bark (including *Betula papyrifera* Marsh., *B. populifolia* Marsh., and *B. cordifolia* Regel) are often little differentiated from each other and from races of this complex in Europe and Asia, and they commonly hybridize in nature. *Betula papyrifera,* paper birch, canoe birch, is transcontinental in distribution across the Boreal Zone, extending south in cool forests at high elevations in the Appalachians. Although individuals of this species are relatively short lived (about 150 years), they sometimes reach a height of 30 m and a trunk diameter of nearly 1 m. Their distinctive features include pinkish to chalky-white exfoliating bark marked with dark, horizontal lenticels; ovate, doubly serrate, acute to acuminate leaves with rounded or cuneate bases; and infructescence scales having relatively wide, rather angular ascending lobes of about the same length. *Betula populifolia,* gray birch, occurs from Quebec to southwestern Ontario and south to Delaware, northern Pennsylvania, and northern Indiana. It is distinguished from *B. papyrifera* by its close bark, deltoid to rhombic leaves with long-acuminate tips, and cone scales with very short central lobes.

The only white-barked birch to enter our range is *Betula cordifolia,* heartleaf birch. This species, sometimes treated as *B. papyrifera* var. *cordifolia* (Regel) Fern., occurs from Labrador and central Ontario to northern New York, Michigan, Wisconsin, and northern Indiana, and south along the Appalachians as small disjunct populations as far as Mount Mitchell in the Black Mountains of North Carolina (listed as *B. papyrifera* in Radford). It is similar in aspect to *B. papyrifera* but differs in its cordate leaves with more lateral veins, reddish bark, narrower and longer infructescence-scale lobes, larger fruits, and other characters. It is found at higher elevations than *B. papyrifera* throughout its range. Its different chromosome number ($2n = 28$ or 56 in *B. cordifolia,* $2n = 56$, 70, or 84 in *B. papyrifera*; Grant & Thompson; Löve & Löve, 1966), plus results from a discriminant analysis of morphological characters (Grant &

Thompson), support recognition of *B. cordifolia* at the species level. This interpretation is also supported by a study of betulin content of the bark of *B. cordifolia* (O'Connell *et al.*).

Populations of a shrubby, small-leafed white birch, *Betula minor* (Tuckerman) Fern., occasionally occur with *B. cordifolia* and *B. glandulosa* (discussed below) from Labrador south to the Gaspé Peninsula and the Laurentian Mountains, Quebec, with disjunct populations in northern New England and the Adirondack Mountains. This birch was treated as a variety of *B. papyrifera* by Tuckerman, as a subspecies of *B. pubescens* by Löve & Löve (1966) and as conspecific with *B. fontinalis* by Scoggan. It has long been suspected of representing a hybrid. Lepage concluded that its holotype represents a hybrid plant, but that Canadian populations, which he named *B. saxophila* Lepage, constitute a natural species. Löve & Löve (1966) determined that plants near the summit of Mount Washington had a chromosome number of $2n = 56$. However, at least one of the putative parents (*B. glandulosa*) has never been reported with a number higher than $2n = 28$, and the other (*B. minor*) has usually been found also to be diploid. Therefore, if *B. minor* actually represents a hybrid, it may be of alloploid origin.

From western Ontario to northeastern British Columbia and south in the mountains of the western United States to northern New Mexico and California, *Betula papyrifera* is replaced by *B. fontinalis* Sarg., water birch, a tall, shrubby race with darker, mostly nonexfoliating bark, smaller leaves, and cone scales with broad, ascending lateral lobes. The name *B. occidentalis* Hooker, often applied to this species, is illegitimate because both the original description and the specimens cited in the protologue are mixed (Dugle, 1969). A fifth species, *B. resinifera* (Regel) Britton, Alaska birch, occurs from central Canada to Alaska. This species resembles *B. papyrifera,* but it is smaller in stature, reaching a height of only about 12 m, and it differs in its more acuminate leaves and in details of the shape of its infructescence-scale lobes.

Two additional species with white bark, *Betula caerulea* Blanch., blue birch, and *B. caerulea-grandis* Blanch., big blue birch, have been a source of confusion and controversy. *Betula caerulea-grandis,* which occurs from southern Quebec to Nova Scotia and in adjacent areas of New England and New York, resembles *B. papyrifera* in size, bark morphology, and general aspect, but its leaves are glabrous with more extended apices and more rounded or strongly cuneate bases, and its infructescence scales, like those of *B. populifolia,* have a short central lobe. *Betula caerulea* is similar in habit but smaller, reaching a height of only 8 or 9 m, and it has somewhat smaller and more sharply cuneate leaves. Sargent (1922) suggested that both of these forms are hybrids of *B. papyrifera* and *B. populifolia,* while Fernald (1922) concluded that *B. caerulea-grandis* was a "good" species, and that *B. caerulea* represented a hybrid between it and *B. populifolia* (cf. Fernald, 1950a). From a morphological analysis of the complex, Brayshaw (1966b) found that *B. caerulea* and *B. caerulea-grandis* fall between *B. populifolia* and *B. papyrifera* in many characters and concluded that the blue birches represent extremes of a hybrid swarm between those species. A paper and thin-layer chromatographic analysis of the northeastern white-barked birches by Koshy and colleagues demonstrated close flavonoid

relationships among *B. caerulea, B. populifolia, B. caerulea-grandis, B. cordifolia,* and *B. papyrifera* and showed patterns supporting this conclusion. However, Brittain & Grant (1967a), Grant & Thompson, and Guerriero and co-workers, in further morphological and cytological studies, concluded that *B. caerulea* and *B. caerulea-grandis* represent hybrids between *B. populifolia* and *B. cordifolia.* Dehond & Campbell's recent multivariate analysis of a single community in Maine containing *B. papyrifera, B. cordifolia, B. populifolia,* and *B. caerulea-grandis* suggested that *B. caerulea-grandis* represents a hybrid between *B. populifolia* and *B. cordifolia,* with *B. papyrifera* apparently not entering into the hybridization. These results have been substantiated by a study of betulin content in the bark of trees of the same population (O'Connell *et al.*).

Section HUMILES W. D. Koch (subsect. *Nanae* (Regel) Winkler), the "dwarf birches," are shrubs of the cold circumpolar region that are characterized by small, rounded leaves with few veins and by staminate catkins that are borne laterally and (usually) singly, enclosed in buds during the winter prior to anthesis. The usually solitary carpellate catkins emerge with new growth from the apical buds of short shoots. *Betula pumila* L., bog birch, an upright spreading shrub to ca. 4 m in height with leaves to ca. 7 cm long, is a common and variable species throughout bogs and fens of cool northeastern North America. A scarcely distinct more northern variety, *B. pumila* var. *glandulifera* Regel (*B. glandulifera* (Regel) Dugle), is marked by pubescent, somewhat gland-dotted branchlets and often smaller, more glandular leaves. This variety occurs from Newfoundland to the Yukon, extending southward in the western mountains to Oregon. A second dwarf species, *B. glandulosa* Mich., is found from Greenland and Labrador to western Canada and south in the Rocky Mountains. It is distinguished by its much smaller (to 3 cm long) leaves, its stems that are warty with large resinous glands, and its ascending lateral infructescence-scale lobes. This species reaches its southernmost limit in the East on the summits of high peaks, including Mount Washington (New Hampshire) and Mount Marcy (New York). A third member of this group, *B. nana* L., usually a prostrate shrub with tiny leaves, is circumpolar across the high latitudes of Europe, Asia, and North America. A similar species, *B. Michauxii* Spach, occurs in Nova Scotia and Newfoundland. It differs from *B. nana* primarily in the shape of the infructescence bracts (often lacking the side lobes) and in its wingless fruits (Fernald, 1950b; Rousseau & Raymond). In a preliminary multivariate analysis of these species, Furlow (1984) found that *B. Michauxii* differs very little from *B. nana* and concluded that it did not deserve specific status. *Betula rupestris,* an intriguing birch apparently related to this complex, was described by Rafinesque in 1819 (p. 229) from northern Kentucky on "the cliffs and on the sandstone rocks of the Kentucky river in Estill County." Although no specimen of this record exists today, Rafinesque's description agrees almost perfectly with that of *B. pumila,* not presently known farther south than central Ohio.

Birches and alders share many features, but they are easily distinguished by the bracts of their infructescences, which are three-lobed and deciduous in *Betula* and five-lobed and persistent in *Alnus.* In vegetative morphology, including the structure of their leaves, buds, shoots, and bark, and their broad-winged fruits, species of *Betula* resemble those of *Alnus* subg. ALNOBETULA.

However, the leaves are distinct in that they lack uniseriate-stalked glandular trichomes (Hardin & Bell). Like the alders, some birches have cut-leaved forms (Hylander, 1957b). In pollen morphology the two genera are distinct, with grains of *Alnus* normally bearing four or five apertures and those of *Betula* most frequently having three and lacking the prominent arci characteristic of alder pollen. Overall, the genus is much more homogeneous morphologically than *Alnus* is.

The birches are a difficult group taxonomically because of their high vegetative variability and frequent hybridization. Particular confusion has centered around the variable white-barked birches of the circumpolar *Betula alba* complex, the North American representatives being considered geographic races of a single species, *B. pubescens* Ehrh. (*B. alba* L.) (e.g., by Fernald, 1902), or separate species or hybrids (see Fernald, 1945b; Grant & Thompson; Hitchcock; Hultén). The response of several American authors (e.g., Britton; Butler) to the observed diversity was to name numerous new species (see Dugle, 1966). Others (e.g., Fernald, 1902) have recognized the American forms as varieties of the European species. Gleason and Gleason & Cronquist (1963) suggested that *B. papyrifera* and *B. pubescens* might better be considered parts of a single circumboreal species, but they, as well as Fernald (1950a) and most other modern authors, have maintained the American plants as separate species. Recent cytological research has begun to elucidate some of the subtle relationships of American representatives of the complex (see the review of Dugle, 1966). Several of the races differ in chromosome number and on the basis of meiotic irregularities (Woodworth, 1931) are possibly of hybrid origin. However, the American *B. papyrifera* is interfertile with both of the European white-barked species, *B. pubescens* Ehrh. (*B. alba*) and *B. pendula* Roth (*B. verrucosa* Ehrh.), even though a sterility barrier exists between the two European species (Johnsson, 1949).

Many morphological and cytological studies have dealt with variation within and among separate and (mostly) mixed populations of the European white-barked birches, *Betula pubescens* and *B. pendula*. The most comprehensive reviews of this work are those of Natho (1959, 1964). Jentys-Szaferowa (1949, 1950, 1952), using simple statistical and graphic methods, analyzed morphological variation in Polish populations, and Gardiner & Jeffers and Gardiner & Pearce, employing multivariate statistics, examined leaf-shape variation in populations in Scotland. These studies have shown both species to be extremely variable and suggest that they hybridize whenever they occur together. Jentys-Szaferowa (1950) noted that, because of this high variability, *B. pubescens* and *B. pendula* cannot be separated on the basis of any single character, but that each one is held together on the basis of combinations of characters and represents a natural group.

The cytogenetics of the European white-barked birches has been studied extensively (see the reviews of Brown & Al-Dawoodie, 1979; Gardiner, 1984; and Johnsson, 1974). Helms & Jørgensen first pointed out that the chromosome number of *Betula pubescens* is $2n = 56$, while that of *B. pendula* is $2n = 28$. This fact was discussed further by Woodworth (1931), and Johnsson (1945) noted the presence of nonchromosomal sterility barriers between the species.

Nevertheless, triploid ($2n = 42$) plants have been widely reported in mixed populations (see Brown & Al-Dawoodie, 1977, 1979; Brown & Williams; Eifler, 1956, 1958; Gardiner & Pearce; Helms & Jørgensen). Lindquist has noted that some of the triploid plants described by Helms & Jörgensen lack intermediate characters and thus might represent autopolyploids.

A result of some of this work has been the formal recognition (e.g., by Gunnarsson) of many simple variants and putative hybrids as separate species or varieties. In a more moderate treatment of the European birches, Lindquist consolidated the variants of *Betula pendula* into three varieties that correspond with major phytogeographic regions. From a study of *B. pubescens* in relation to the subspecies recognized in *Flora Europaea* (Walters), Gardiner (1984) concluded that two main races of that species occur in Europe, an arctic and southern montane group corresponding to subsp. *tortuosa* (Ledeb.) Nyman, and a common lowland form corresponding to subsp. *pubescens*. A third subspecies recognized in *Flora Europaea*, subsp. *carpathica* (Willd.) Ascherson & Graebner, differs little from subsp. *tortuosa*.

The taxonomy of the *Betula alba* complex has long been complicated by disagreement over the correct name of *B. alba* itself, as well as those of the other white-barked birches with which it occurs. According to Winkler (1904, 1930), Linnaeus circumscribed *B. alba* in such a way that he included both of the white-barked species of northern and central Europe in his concept (although Linnaeus's name "Betula foliis ovatis acuminatis serratis" and the listed synonym from *Flora Lapponica*, "Betula foliis cordatis serratis," together with his herbarium material, seem in fact to apply well to only one element of the complex). The major components of *B. alba* were separated by Roth as *B. alba* and *B. pendula* Roth. However, European authors have since mostly used the later name *B. pubescens* Ehrh. for the species with pubescent leaves and upright branches (*B. alba* as interpreted by Roth) (see Fernald, 1945b, p. 309, who condemned "the very doubtful Germanic practice of rejecting all Linnaean names of European species if they included what are now considered two or more species . . ."). Many nineteenth-century workers (e.g., W. D. J. Koch; Lamarck & De Candolle) at the same time incorrectly applied the name *B. alba* to what should have been called *B. pendula*, and many (although not all) recent systems substitute *B. verrucosa* Ehrh. for *B. pendula* (see Fernald, 1902, 1945b). Recent European authors have mostly used *B. alba* in the sense of a "collective species" or *Grossart* (a named species complex; *cf.* Natho, 1964; Winkler, 1930), ignoring its nomenclatural priority for one of the elements of that complex. In the present treatment, the name *B. pubescens* has been employed to follow prevalent current usage, pending final clarification of the issue.

Taxonomic confusion also exists with regard to the dwarf birches (see Furlow, 1984; Lepage). The various North American taxa of this complex have been combined and split into a large number of species and infraspecific taxa. The most comprehensive recent analysis of these problems is found in the work of Dugle (1966), who studied the relationships and hybridization patterns among the various taxa occurring in western Canada. Using statistical analyses of morphological characters in combination with chromatographic and cytological procedures, Dugle recognized and described the variation patterns of two species

(*Betula glandulosa* and *B. glandulifera*) and four hybrids of dwarf birches. Similar work is needed for the eastern American and European segments of the complex, followed by a comprehensive taxonomic revision of the entire group.

Several studies have been made of the vegetative variability of the three southeastern species. Coyle and colleagues (1983a) have described clinal variation and population differentiation in *Betula nigra* based on measurements of leaf characters. Dancik and Dancik & Barnes (1971) have shown that the bark of *B. alleghaniensis* varies from light colored and exfoliating to dark and close in certain populations. Trees exhibiting the latter characters were at first thought to represent hybrids between *B. alleghaniensis* and *B. lenta* but after study were judged to be dark-barked variants of *B. alleghaniensis*. Further work (Dancik & Barnes, 1975; Sharik & Barnes, 1979) has shown that the two species vary considerably, both within and among populations (often more so within populations), but with discernible trends for many characters over latitudinal and altitudinal gradients.

Wood of the dwarf northern birches, like that of the shrubby alders, exhibits primitive (juvenile) characters (e.g., many small vessels and numerous tracheids), while that of species of sects. Costatae and Betula is more specialized (Hall). The most specialized wood is present in members of sect. Betulaster Regel (cf. Roskam).

The staminate inflorescences of *Betula* are similar to those of *Alnus* except that they lack the two tertiary bracts subtending the cymules (Abbe, 1935, 1938, 1974). As in *Alnus,* the number of stamens and tepals in each flower differs among the species—i.e., generally three or four in members of sect. Costatae, two or three in sect. Betula, and one or two in sect. Humiles. In sect. Betulaster, the number of stamens has been reduced to two, but four tepals have been retained, a condition seen also in *Alnus* but not elsewhere in *Betula* (Abbe, 1935). The carpellate cymules of *Betula* differ from those of all other Betulaceae in that they usually retain all three flowers; the secondary one is absent in the other genera (Abbe, 1935).

As in *Alnus,* various lines of *Betula* have become specialized in the grouping, number, and position of the staminate and carpellate catkins (Hjelmqvist, 1948; Jäger). The staminate catkins are produced the season before blooming in all sections except sect. Humiles. The carpellate ones develop with the new growth in all sections. The number of both staminate and carpellate catkins in each cluster has been reduced from four or more in subg. Betulaster to one in sect. Humiles (cf. Jäger). Accompanying this reduction are alterations in branching that place the staminate catkins (which occur near the ends of branches and above the carpellate clusters in subg. Betulaster and sects. Costatae and Betula of subg. Betula) below the terminal carpellate ones on short shoots in sect. Humiles (Jäger). These changes parallel modifications, interpreted as adaptations to cold climates, seen in *Alnus* subg. Alnobetula (Furlow, 1979).

Little chemosystematic work has been attempted with woody plants in general in comparison with herbaceous groups. However, a surprising number of studies have been undertaken in *Betula.* An early flavonoid study was conducted by K. E. Clausen (1960b) to identify hybridization between *B. papyrifera*

and *B. pumila*. Other work, in addition to that of Koshy and colleagues (described above), has included an extensive series of investigations of northern European birches by Pawlowska (1980a–c, 1982a, 1982b, 1983a, b) to demonstrate relationships of flavonoid occurrence among various species, species segregates, and putative hybrids. An electrophoretic analysis of pollen proteins in *B. populifolia* by Payne & Fairbrothers showed a high level of variation in proteins among populations in that species and suggested that local population differentiation was occurring. In a study of ten *Betula* species of the Soviet Far East, Baranov and co-workers found triterpene data to be taxonomically useful in the identification and separation of groups and subgroups of various species.

Species of *Betula* form a polyploid series, with chromosome numbers of $2n = 28, 56, 70, 84$, and 112, plus dysploid numbers in some hybrids (Woodworth, 1929b; Dugle, 1966; Poucques; Wetzel, 1927, 1928, 1929; Barnes & Dancik). Of the southeastern species, *B. nigra* and *B. alleghaniensis* are diploids ($2n = 28$), while *B. alleghaniensis* is hexaploid ($2n = 84$). Meiosis is normal in the diploids and somewhat abnormal in *B. alleghaniensis* (Woodworth, 1929b). Although the European *B. pubescens* (*B. alba*) and two of its northeastern American races, *B. papyrifera* and *B. fontinalis,* form a circumpolar complex having distributional and morphological patterns similar to those of *Alnus incana,* these birches represent different polyploidy levels ($2n = 56$, 70, and 84, respectively), lending support to their continued treatment as separate species. The European species, *B. pendula* Roth, and its American and Asian counterparts, *B. populifolia* and *B. japonica* Sieb., are diploids ($2n = 28$), but these forms are more differentiated morphologically than are the members of the *B. pubescens* group. Consequently, there has been little tendency to treat them as conspecific. In both complexes the segments should be examined in relation to modern species concepts to determine whether they might better be treated as a single species.

The birches are anemophilous and produce large quantities of pollen (Wodehouse, 1935). In all subgroups of the genus, the carpellate catkins appear with the new growth, and anthesis occurs as the leaves unfold. Achenes are produced in large numbers and are carried for considerable distances by the wind.

Natural hybridization is common (Alam & Grant; Johnsson, 1945), and many of the resulting hybrids have been named (see L. P. V. Johnson; Kartesz & Kartesz; Winkler, 1904). In eastern North America *Betula alleghaniensis* and *B. lenta* have been shown to hybridize (Sharik & Barnes, 1971). These species, as well as *B. papyrifera* and *B. populifolia,* also hybridize with *B. pumila* in the North where their ranges overlap (Cousins). Through artificial crosses hybridization between *B. papyrifera* and *B. populifolia* has been studied by Alam & Grant, who found the progeny to resemble *B. papyrifera* more closely than *B. populifolia* in juvenile leaf characters. Seeds from single trees of various taxa of *Betula* often give rise to offspring of two or more ploidy levels, and there "appears to be little barrier to cross fertilization between *Betula* plants with different levels of polyploidy" (Grant, 1969, p. 81). He suggested that this feature may have permitted the genus to take advantage of new ecological niches that opened up following the Pleistocene.

The earliest pollen and leaf material of *Betula* is from the Upper Cretaceous,

and fossils of *Betula* are widespread and highly diversified by the Middle Eocene (Crane & Stockey). Differentiation of subgenera and sections appears to have occurred largely in response to major climatic differences (Jäger; Kikuzawa). A cladistic analysis of the birches by Roskam, done as part of a study of coevolutionary patterns in the birches and their gall-midge parasites, indicated that sect. COSTATAE is the most plesiomorphic subgroup and the sister group of *Alnus* subg. ALNOBETULA, with which the tree birches share many characters. However, it seems unlikely that *Betula* sect. COSTATAE is closely related to *Alnus* subg. ALNOBETULA. If the shrubby growth form indeed represents adaptation to cold climates, as is strongly suggested by morphological and phytogeographic patterns in both genera, it is improbable that unspecialized birches could have evolved directly from one of the most highly specialized groups of alders, or vice versa. In a preliminary cladistic analysis by Furlow (1983), all of *Alnus* and all of *Betula* appear as sister groups. Within *Betula,* sect. COSTATAE is most closely related to sect. BETULASTER.

Birches serve as important sources of food for browsing animals (LeResche & Davis; Oldemeyer). Palo, Pehrson, & Knutsson and Palo, Sunnerheim, & Theander have shown that phenolic compounds become much more concentrated in the twigs and bark of white-barked birches during the winter and have correlated this fact with striking examples of weight loss and reduced food consumption in vertebrate herbivores feeding on birch twigs and branches in the winter. They suggested that phenolic compounds may constitute a major chemical defense in birches against browsing animals.

In areas recently exposed by logging or natural causes, *Betula papyrifera* and *B. alleghaniensis* often exhibit symptoms of distress and gradually die from the top downward. This occurrence, known as "decadence," has generally been attributed to suddenly changing environmental conditions. During the 1930's, a disease with similar symptoms (termed "dieback") appeared in New Brunswick and rapidly spread throughout the Northeast, although there had been no alteration of the surrounding forest. By 1905 at least 80 percent of the merchantable birch had been killed in the Maritime region of Canada to as far west as New Hampshire (Clark; Clark & Barter). Dieback, which affects *B. alleghaniensis* more severely than *B. populifolia,* and which in Europe and in ornamental plantings also affects especially *B. pendula,* has since spread westward through New York, Ontario, Michigan, and Minnesota. Various explanations have been proposed, but thus far no single climatic or biotic cause has been identified. It has been suggested by Ball & Simmons and Houston that a population is first weakened by adverse environmental conditions, such as a period of drought, then is invaded and eventually decimated by the bronze birch borer, *Agrilus anxius* Gory, a native buprestid beetle. Others (e.g., Berbee; Cooper & Massalsk) believe, on the basis of the nature of dieback symptoms, that the initial causative agent of decline may be a virus, with borer invasion following in the weakened trees.

Many insect species feed on or otherwise affect birches, the most detrimental being the bronze birch borer. Others include the gypsy moth, tent caterpillars, leaf miners, and scale insects. Fungal diseases result in the destruction of large numbers of trees and are therefore of considerable economic consequence

(Hepting). The most important of these include heartwood rots caused by various species of *Fomes* and *Poria,* especially *Fomes ignarius* (L.) Kickx (Basham & Morawski; Campbell & Davidson), and nectria canker (*Nectria galligena* Bres.), the most damaging external stem disease of yellow birch and paper birch (Hepting).

The pollen of birches, in regions where they are numerous, is a significant cause of hay fever (Lewis & Imber; Lewis *et al.*; Løwenstein *et al.*; Wodehouse, 1945). During the past two decades considerable progress has been made in Europe to elucidate the basis of this ailment (Apold *et al.*; Berlin; Vik & Elsayed; Vik *et al.*). This research has revealed that the allergenic reaction to *Betula* pollen is related to that caused by *Alnus* and *Corylus* pollen. The responsible allergens have been partly identified (Dalen & Voorhorst; Løwenstein *et al.*). It has been shown that in children, birch-pollen allergies are sometimes related to food allergies (Dreborg & Foucard; Halmepuro *et al.*; Lahti *et al.*; Løwenstein & Eriksson). Birch sap has also been shown to cause a contact dermatitis in persons sensitive to birch pollen (Lahti & Hannuksela).

The wood of the birches has many uses (reviewed by Lines). In eastern North America *Betula alleghaniensis* and *B. lenta* are important sources of hardwood timber employed in the manufacture of doors and windows, flooring, cabinetry, interior molding, wood paneling, barrels, shoe lasts, furniture, and plywood. These and other species, especially *B. papyrifera,* are also widely used for making small specialty products, including wooden toys, athletic equipment, broom handles, clothespins, ice-cream sticks, spools, bobbins, and toothpicks. Wood of various species has long been utilized to make charcoal for gunpowder and for filtration purposes.

In the northern Appalachians *Betula lenta* is sometimes tapped during the spring in the same way sugar maple trees are tapped, the collected sap being fermented to produce a naturally carbonated birch beer. A tea is made from the bark and twigs of this species by steeping them in hot water (Fernald *et al.*; Sargent, 1896). *Betula lenta* was formerly a major commercial source of methyl salicylate, the chief constituent of wintergreen oil, widely used as a flavoring and as a component of pharmaceuticals, including aromatic cascara sagrada fluid extract (sweet cascara). Its chief medicinal use has been as a rubefacient and, in the past, as an antirheumatic (Lewis & Elvin-Lewis). Today, methyl salicylate is largely produced synthetically. Infusions of the bark of various birch species were widely used by North American Indians as treatments for infections, colds, pulmonary problems, burns, leukorrhea, and other ailments (Lewis & Elvin-Lewis; Moerman). Twigs of *Betula lenta* and *B. alleghaniensis* have been used in modern times as chewing sticks for cleaning the teeth (Lewis & Elvin-Lewis).

A pyroligneous oil is obtained by distillation from the bark and wood of *Betula pendula* and other species. This material has been widely used in northeastern Europe in the preparation of leather and in the manufacture of lotions, ointments, and medicines. Birch wood is a common source of high-quality firewood and of pulp for manufacturing paper in regions where the trees are plentiful. Birch bark, rich in oil and starch, has been used for centuries by people in times of famine as a source of food. Many species, especially those

with white bark (*B. pendula, B. pubescens, B. populifolia,* and *B. papyrifera*), as well as *B. nigra,* are utilized horticulturally (of these, *B. pendula* is by far the most widely used in the United States). The bark of *B. papyrifera,* which is waterproof and easily workable because of its betulin and oil content, was extensively employed by northern North American Indians as a covering material for canoes, houses, and bundles, and as a material for making various articles of clothing.

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Subfamily CORYLOIDEAE (Regel) Koehne

Tribe Carpineae Döll

3. **Carpinus** Linnaeus, Sp. Pl. **2:** 998. 1753; Gen. Pl. ed. 5. 432. 1754.

Small [to large] usually spreading trees, mostly with a single trunk; branching mostly deliquescent; trunk and branches irregularly longitudinally ridged and fluted, the branchlets and twigs conspicuously distichous; twigs differentiated into long and short shoots. Bark close, thin, smooth, bluish- to brownish-gray, becoming thicker and scaly or furrowed in age, the lenticels generally inconspicuous; young twigs glabrous or sparingly pubescent; leaf scars narrowly crescent shaped to suboval, with 3 circular to elliptic vascular bundle scars; winter buds sessile, ovoid, 4-angled in cross section, usually appressed, the apices acute, with many smooth, imbricate scales; wood fine grained, nearly white to light brown, extremely hard, very heavy; pith circular to slightly angular in cross section. Leaves distichous, borne on long and short shoots; blades thin, narrowly ovate to ovate, elliptic, or obovate, doubly serrate [to

FIGURE 3. **Ostrya** and **Carpinus.** a–j, *O. virginiana*: a, flowering branchlet, pendent staminate catkins above, carpellate catkin partly hidden by expanding leaves below, ×½; b, adaxial side of staminate cymule with bract (composed of primary bract united with 2 secondary ones) visible behind, portion of axis of catkin below, ×8; c, d, 2 views of stamens, showing division of anther and upper part of filament into halves, ×15; e,

serrulate], glabrous to tomentose abaxially, sometimes with small glands abaxially; secondary venation craspedodromous, divergent and straight; leaves in bud concave, plicate, not conduplicate; stipules broadly ovate. Staminate catkins lateral, from axillary buds on short shoots, solitary [or in small racemose clusters], borne below the carpellate catkins, formed the previous growing season and [exposed or] enclosed in buds during the winter, expanding with the leaves, the scales broadly ovate [to elliptic], relatively uncrowded [to crowded], each consisting of 3 fused bracts; carpellate catkins terminal on short shoots from leafy new growth, solitary, developing at the same time as the staminate ones, enclosed within buds during the winter and expanding with the leaves, more or less erect, uncrowded [to crowded], with paired flowers subtended by a primary scale and each surrounded by a 3-lobed scale consisting of 3 fused bracts. Staminate flowers 3 per scale, each flower consisting of 3(–6) stamens, several such clusters crowded together on a pilose torus at the base of the scale; stamens short, the anthers divided into 2 1-locular parts, pilose at the apex, the filaments often divided partway to the base; pollen grains spheroidal to slightly flattened, 20–45 μm in diameter, slightly aspidote, with 3(–6) circular to slightly elliptic equatorial apertures. Carpellate flowers sessile, 2 per primary scale; ovary 1, 2-locular, with 2 linear styles; perianth of several scalelike tepals, these adnate to the ovary and apparent as a membranaceous or short-fringed margin at the apex; sometimes with 1 or more staminodes; ovule 1 by abortion, bitegmic. Infructescences elongate, pendulous, consisting of a loose racemose [to densely imbricate] cluster of pairs of expanded, [(1- to)] 3-lobed and variously toothed foliaceous bracts, each bract subtending a single fruit, splitting away with the adnate fruit. Fruits small, ovoid, longitudinally ribbed nutlets, usually crowned with the persistent tepals and styles, maturing and dispersed the same season as pollination; pericarp relatively thick and bony; seeds with membranaceous testa and somewhat thickened cotyledons; germination epigeal. Chromosome numbers $2n = 16, 32, 64$. LECTOTYPE SPECIES: *Carpinus Betulus* L.; see N. L. Britton, N. Am. Trees, 241. 1908; N. L. Britton & A.

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adaxial side of carpellate cymule, showing primary bract (1) and 2 flowers (only styles visible), each with sheath composed of secondary bract united with 2 tertiary ones, ×15; f, carpellate flower at anthesis, showing 2 receptive styles and hardly developed ovary crowned by rudimentary perianth, ×15; g, carpellate cymule in young fruit, inflated surrounding bracts (secondary united with tertiary) removed from developing fruit at right to show persistent styles and collarlike perianth topping ovary, ×5; h, branchlet with nearly mature infructescence, each fruit surrounded by inflated bracts (cf. e, g), ×½; i, mature fruit with persistent rudimentary perianth and styles at top, ×4; j, seed, with aborted ovule at upper left, ×4. k–q, *C. caroliniana*: k, adaxial side of staminate cymule, showing stamens of 3 flowers with bract (composed of united primary and secondary bracts) behind, portion of axis of catkin below, ×8; l, stamen, showing half-anthers and partly divided filament, ×15; m, carpellate cymule, from adaxial side, showing primary bract (1) and 2 flowers (only styles visible), each surrounded by 3-lobed bract composed of a secondary bract (2) united with 2 tertiary ones (3), ×15; n, carpellate flower, the hardly developed ovary with minute perianth, ×15; o, branchlet with nearly mature infructescences, each fruit subtended by 3-lobed bract, ×½; p, mature fruit adnate to 3-lobed bract (united secondary (2) and tertiary (3) bracts), portion of axis splitting away, ×1½; q, mature fruit topped by accrescent perianth and persistent styles, ×4.

Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **1**: 606. 1913. (The Latin name used by Pliny and other ancient writers for the hornbeam; possibly derived from *carpentum,* the name of a horse-drawn vehicle made from its wood.)—HORNBEAM, IRONWOOD.

A genus of about 25 species of small to large trees mostly of the North Temperate Zone, but with a few extending into Central America along the Sierra Madre and in the Old World in the mountains from the North Temperate Zone to India and Iran. *Carpinus Betulus* is a large and important forest tree throughout much of Europe (where it attains trunk diameters of up to 4 m). In mountainous Mexico and Central America *C. tropicalis* (J. D. Sm.) Lundell forms a dominant canopy component. Some of the Asian species also become large trees. However, *C. caroliniana* Walter subsp. *virginiana* (Fern.) Furlow, of the northeastern United States and adjacent Canada, and subsp. *caroliniana,* found throughout the Coastal Plain (Fernald, 1935; Furlow, 1987b), consist of smaller forms of the forest understory, often near streams, where they occupy a subdominant position.

Carpinus was treated taxonomically by Spach, De Candolle, and Winkler (1904). De Candolle divided the family Corylaceae into tribes CARPINEAE and CORYLEAE, the latter containing only *Corylus* (as followed in the present treatment). He further divided *Carpinus* into two genera, *Carpinus* and *Distegocarpus* Sieb. & Zucc., the latter an Asian group (*D. japonica* Blume, *D. cordatus* Blume) characterized by elongate, stipitate, more densely imbricate staminate floral bracts and crowded infructescences composed of numerous broad unlobed scales (as opposed to broadly ovate, subsessile, more or less uncrowded staminate bracts and open infructescences of relatively few distinctly three-lobed scales in *Carpinus*). Winkler (1904) treated these segregates as sections of *Carpinus,* and this remains the most frequently used treatment today. In a further revision of the genus (1914), he named a number of new species and varieties, based largely on the shape and size of the leaves and the infructescence bracts. Rafinesque modified the name of the genus, which he considered too similar to *Pinus,* to *Carpinum,* and this variant is sometimes cited as a synonym. Additional study is needed to determine whether sect. DISTEGOCARPUS (Sieb. & Zucc.) Sarg. is distinct enough to warrant continued recognition.

Numerous Asiatic species of *Carpinus* have been described in recent decades. In an early enumeration of Chinese *Carpinus,* Hu (1933) reported 23 species. Lee (1935) listed 24 species in *Forest Botany of China,* and 52 in the supplement to this work (1973). In *Flora Reipublicae Popularis Sinicae* Li & Cheng listed 25 species, together with an additional 15 infraspecific taxa. Although it is doubtful that all of these taxa deserve formal recognition, some of them appear to represent good species. The genus as a whole is in need of a comprehensive taxonomic revision.

In North America *Carpinus* consists of two species, *C. caroliniana* Walter and *C. tropicalis* J. D. Smith, each with several geographic races (Furlow, 1987a). Fernald (1935) first distinguished an Atlantic and Gulf Coastal Plain race, with small, blunt-toothed leaves, from the widespread Appalachian and continental form. Furlow (1987a) analyzed this complex using multivariate

statistics and concluded that the Latin American hornbeams constitute a divergent group, most likely not derived from the species in the eastern United States, and recognizable as a separate species. The Coastal Plain populations of the United States were shown to form a distinctive and cohesive subgroup of *C. caroliniana.* This and the Appalachian race were recognized formally at the level of subspecies.

Carpinus caroliniana, American hornbeam, ironwood, blue beech, is easily recognized by its smooth, gray, often fluted stems, normally ovate to elliptic sharp-toothed leaves, and racemose infructescences of pairs of uncrowded, leaflike, three-lobed bracts, each subtending a small triangular nutlet. The staminate (but not the carpellate) catkins develop in the autumn, although they are enclosed in buds throughout the winter prior to anthesis. The carpellate catkins are produced on the first new growth in the spring. Both the staminate and carpellate catkins (except in sect. DISTEGOCARPUS) are much more uncrowded than those of *Alnus* or *Betula.*

Leaves of *Carpinus* closely resemble those of *Ostrya.* Both lack peltate scales (sessile glands), and they have similar kinds of trichomes. However, they differ in the structure of their stipitate glands: in *Carpinus* the stalks are uniseriate, rather than multiseriate, and the heads are more globose (Bell *et al.*; Hardin & Bell). The color and degree of development of these glands in *C. caroliniana* were shown by Furlow (1987a, b) to be of value in characterizing the subspecies.

The wood, which overall has been regarded as rather advanced in the Betulaceae, has both primitive features (e.g., numerous vessels of small diameter) and advanced ones (e.g., spiral thickenings on the vessels, homogeneous rays) (Hall). In some characters (e.g., structure of the perforation plates), relatively primitive states are present in some species and more advanced ones in others. Hall concluded that true tracheids were absent in *Carpinus,* although he noted fiber tracheids in all genera of the family. Recently, Yagmaie & Catling reported the presence of true tracheids in the wood of *Carpinus.*

Staminate inflorescences of *Carpinus* and *Ostrya* are much more difficult to interpret than those of members of the Betuloideae because the flowers lack tepals and the cymules lack tertiary bracts (see Abbe, 1935, 1974). In *Carpinus* the catkins consist of clusters ("partial inflorescences") of about 18 stamens. From the patterns observed in the Betuloideae and in *Corylus,* and from MacDonald's anatomical observations in *Ostrya* (see below under *Corylus*), such clusters have been interpreted as highly reduced cymules of three flowers, each consisting of six stamens (Abbe, 1974). The carpellate cymules consist of two ovaries subtended by one primary, two secondary, and four tertiary bracts (Abbe, 1935). As the infructescence develops, the primary bract abscises and the united secondary and two tertiary bracts associated with each fruit develop into a characteristic wing by which the fruits are dispersed (see FIGURE 3p).

Species of *Carpinus* form a straightforward polyploid series of $2n = 16$, 32, and 64 (in *C. caroliniana,* $2n = 16$).

In most species both the staminate and carpellate catkins are produced along with growth of the new leaves. The fruits, attached to expanded winglike bracts that dehisce from the infructescences with them, are dispersed by the wind.

The paleobotanical history of the genus has been reviewed by Crane (1981)

and by Berger. Fossils referred to the Coryloideae first appear in the Paleocene. The genus *Paleocarpinus* Crane, from the upper Paleocene, morphologically links *Carpinus* with *Corylus* on the basis of fruit and bract characters (Crane, 1981, p. 131). Crane proposed that this fossil "may approach the generalized *Carpinus* form envisaged by Hjelmqvist as having given rise to the extant genera of Coryleae." He further showed that modern betulaceous characters began to differentiate in the Upper Cretaceous, with genera such as *Carpinus* greatly diversifying in the late Paleogene and early Neogene, and concluded (p. 131) that this shows that the "strong morphological adaptation for dispersal exhibited by most extant species" had not developed before that time. He proposed that the primary diversification took place in Eurasia, perhaps in relation to vegetation changes following climatic deterioration during the Eocene and Oligocene (cf. Wolfe, 1973).

The origin of populations of *Carpinus* in the mountains of Mexico and Central America (Hernández X. *et al.*) has been the subject of considerable speculation. Some workers (Deevey; Dressler; Miranda & Sharp) considered these populations to be closely related to those of the eastern United States, while others (e.g., Martin & Harrell) emphasized obstacles to the dispersal of mesophytic plants between these areas. Furlow (1987a, b) has shown by means of multivariate analyses that the taxa in Latin America are distinct morphologically and concluded on this basis, as well as on that of phytogeographic evidence, that Latin American *Carpinus* has more likely been derived from an extinct western taxon. Clinal variation and population differentiation have been demonstrated for several characters of *C. caroliniana* (Wardell & Winstead; Winstead *et al.*). Furlow (1987a) showed that these and other characters vary geographically in complex ways, and that the patterns are related to climatic factors—in different ways in different regions.

There are no serious insect pests or fungal pathogens associated with *Carpinus,* although many fungi including mildews and rusts attack the leaves (Hepting). Sargent (1896) listed a variety of insects known to feed on the leaves of members of the genus.

The very hard wood of *Carpinus* has been used, especially in Europe (where the trees are larger), for making mallet heads, tool handles, levers, and other small, hard, wooden objects. It has also been employed to make high-quality charcoal for use in manufacturing gunpowder. The branches are utilized extensively in Europe for fuel. *Carpinus Betulus* and (less frequently) *C. caroliniana* are cultivated as ornamentals, the former being available in a number of cultivars.

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Under family references see ABBE (1935, 1974); BELL *et al.*; CANDOLLE; CRANE (1981); DEEVEY; DRESSLER; HALL; HARDIN & BELL; HEPTING; HERNÁNDEZ X. *et al.*; LEE (1935, 1973); LI & CHENG; MACDONALD; MARTIN & HARRELL; MIRANDA & SHARP; RAFINESQUE; WINKLER (1904); WOLFE (1973); and YAGMAIE & CATLING.

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4. **Ostrya** Scopoli, Fl. Carniolica, ed. 2. **2:** 243. 1772, nom. cons.

Small to medium-sized, usually spreading trees, mostly with a single trunk; branching mostly deliquescent; trunks and branches terete, the branchlets and twigs conspicuously distichous; twigs differentiated into long and short shoots. Bark thin, light brownish gray to light brown, breaking into slender, shaggy vertical shreds, the lenticels generally inconspicuous; young twigs glabrous or sparingly pubescent; leaf scars narrowly crescent shaped to suboval, with 3 circular to elliptic vascular bundle scars; winter buds sessile, ovoid, somewhat laterally compressed, divergent, the apices acute, with many longitudinally striate imbricate scales; wood fine grained, nearly white to light brown, extremely hard, very heavy; pith circular to slightly angular in cross section. Leaves distichous, borne on long and short shoots; blades thin, narrowly ovate to ovate, elliptic, or obovate, doubly serrate [to serrulate], glabrous to abaxially tomentose; secondary venation craspedodromous, the veins divergent and

straight; new leaves in bud concave, plicate, not conduplicate; stipules broadly ovate. Staminate catkins terminal on branchlets, [solitary or] in small racemose clusters, formed the previous growing season and exposed during the winter, expanding with the leaves, the scales relatively uncrowded, broadly ovate, each consisting of 3 fused bracts; carpellate catkins terminal on short shoots from leafy new growth, below the staminate, solitary, developing at the same time as the staminate, enclosed within buds during the winter and expanding with the leaves, more or less erect and uncrowded, the scales 3 fused bracts, these later completely fusing so as to enclose the young fruits completely in bladderlike involucres. Staminate flowers 3 per scale, each consisting of 3(–6) stamens, several such clusters crowded together on a pilose torus at the base of the scale; stamens short, the anthers divided into 2 1-locular parts, pilose at the apex, the filaments often divided partway to the base; pollen grains spheroidal to slightly flattened, 20–45 μm in diameter, slightly aspidote, with 3(–6) circular to slightly elliptic equatorial apertures. Carpellate flowers sessile, 2 per scale; ovary 1, 2-locular, with 2 linear styles; perianth of several scalelike tepals, these adnate to the ovary and apparent as a membranaceous or short-fringed margin at the apex; sometimes with 1 or more staminodes; ovule 1 by abortion, bitegmic. Infructescences consisting of loosely imbricate, pendulous, strobiloid clusters of closed bladderlike involucres derived from the encircling bracts of each flower in the catkins, each bract enclosing and deciduous with a single fruit. Fruits small, ovoid, longitudinally ribbed nutlets, maturing and dispersed during the same season as pollination, often crowned with the persistent tepals and styles; pericarp relatively thick and bony; seeds with membranaceous testa and somewhat thickened cotyledons; germination epigeal. Chromosome number $2n = 16$. TYPE SPECIES: *Ostrya carpinifolia* Scop. (The Greek name used by Theophrastus for a tree with very hard wood; from the Greek *ostryos,* "a scale," in reference to the scaly catkins.)—HOP HORNBEAM, IRONWOOD.

About five species of small trees of the North Temperate Zone. *Ostrya carpinifolia* is a common and important forest tree throughout southern Europe. In North America the genus consists of small trees of the northeastern deciduous forest and the mountains of the southwestern United States and adjacent Mexico, south to northern Central America.

Ostrya was included as a single species of *Carpinus* (*C. Ostrya*) by Linnaeus. Miller accepted this generic concept, but he separated the American species (as *C. virginiana* Miller) from the European; Michaux treated it as *C. Ostrya americana.* The genus was segregated from *Carpinus* in 1772 by Scopoli, who named the common European tree *Ostrya carpinifolia. Ostrya* has since mostly stood as a separate genus, yet on the basis of its inflorescences, infructescences, and vegetative features, the two genera are closely allied. Willdenow, in the fourth edition of *Species Plantarum,* named the American species *O. virginica.* Spach (1842b), in a revision of the genus, recognized two species, *O. italica* Micheli (including all the European forms) and *O. virginica* Willd. De Candolle also recognized these species but correctly selected the earlier name, *O. carpinifolia,* to designate the former. In 1873 K. Koch transferred Miller's name to *Ostrya.* Winkler submerged both *O. virginiana* (Miller) K. Koch and *O.*

carpinifolia as subspecies of *O. italica* but recognized the western North American *O. Knowltonii* Cov. as separate. Rafinesque, in *Florula Ludoviciana,* substituted the name *Zugilus* for *Ostrya* because he believed the name to be too similar to *Ostrea.* Four species are listed for China by Lee (1973) and Li & Cheng, although some of these may be found to be too indistinct to deserve specific status.

Ostrya virginiana is a common tree in North America from Nova Scotia to eastern Manitoba, south to Virginia, northern Georgia, Tennessee, and Oklahoma, with a disjunct population in the Black Hills (South Dakota). Although frequent in the Northeast, *O. virginiana* is seldom a major forest component. There, like *Carpinus caroliniana,* it usually occupies a subdominant position in the understory (although Greenidge has reported that the species is nearly absent from closed old-growth forests in Nova Scotia). Unlike *Carpinus,* it is characteristic of drier or better-drained, more upland sites. It is seldom seen in wet areas. *Ostrya virginiana* is much less abundant in the Southeast than farther north (Duncan, Radford), occurring—when present at all—mostly in the mountains and Piedmont.

The leaves of *Ostrya virginiana* are similar to those of *Carpinus caroliniana,* as are its infructescences and fruits, except that the infructescences are somewhat more compact, with the bracts fused into bladders that completely enclose the fruits. As in *Carpinus,* only the staminate catkins develop in the autumn, although in *Ostrya* these occur in small clusters and are exposed during the winter near the tips of lateral branchlets (short shoots). Also as in *Carpinus,* the carpellate and staminate catkins are loosely arranged at anthesis. One of the most characteristic field characters of *O. virginiana* is its light brownish-gray bark, which shreds into thin, narrow vertical strips. In the winter the trees are distinctive in their numerous small terminal clusters of dormant catkins (absent in *Carpinus caroliniana*).

Coastal Plain populations of *Ostrya virginiana* are represented by a small-leaved and somewhat pubescent geographic race (var. *lasia* Fern.). However, the *O. virginiana* complex has not been studied in detail. Two shrubbier species occur in the Southwest: *O. Knowltonii* Cov. is found in mountains and canyons from southwestern Texas to southeastern Utah (including both rims of the Grand Canyon), and *O. chisosensis* Correll occurs in the Chisos Mountains in Big Bend National Park in southwestern Texas. These two species differ somewhat from each other and from *O. virginiana* in characters of leaf shape, leaf margin, and plant pubescence. However, no comprehensive study has considered the distinctness of these species in terms of their variation patterns or their relationships to other North American taxa.

Additional populations of *Ostrya* occur in the eastern and western mountains of Mexico and northern Central America. Rose believed these segments to differ significantly from *O. virginiana* and named the Mexican group, characterized by more narrowly lanceolate and more gradually acuminate leaves, *O. mexicana* Rose. He called the southern group, with similar features but somewhat broader and more pubescent leaves, *O. guatemalensis* Rose. However, in current work (e.g., Nee) these forms are usually treated as conspecific with *O. virginiana.* The Latin American representatives are especially in need of critical taxonomic examination. The morphological differentiation and pa-

leoecology of these segments, as well as of *O. Knowltonii* and *O. chisosensis,* need to be examined in relation to the complex as a whole.

Although *Ostrya* shares many vegetative features with *Carpinus,* its habit is more treelike. As in *Corylus* but not *Carpinus,* the stipitate glands of the leaves have multiseriate rather than uniseriate stalks, and these bear more elongate heads, features not seen in other Betulaceae (Hardin & Bell). The wood is similar to that of *Carpinus,* but the vessels are of a more specialized type, with largely simple perforation plates (Hall). The genus is seen by Hall as the most advanced of the family on the basis of wood structure.

The inflorescence and flower structure of *Ostrya* is also similar to that of *Carpinus,* except that in the infructescences the secondary and two tertiary bracts of each floret are fused into a sac that envelops the fruit, rather than a flat wing that subtends it (Abbe, 1935, 1974). Even though direct evidence was lacking, Abbe (1935) hypothesized that the clusters of stamens found in staminate catkins of *Carpinus* and *Ostrya* represented the three reduced florets of a cymule comparable to those seen in the Betuloideae. This position was recently supported by the work of MacDonald, who demonstrated three growth areas in the primordia of the staminal groups in developing catkins.

All species of *Ostrya* for which counts have been made have a chromosome number of $2n = 16$.

Unlike *Carpinus,* in most species of *Ostrya* the staminate catkins are produced the season before anthesis and exposed during the winter. The carpellate catkins develop in the spring with the new shoots, with anthesis occurring as the leaves are forming. Dispersal is as in *Carpinus,* except that the bracts form closed bladderlike structures rather than flat wings.

The evolution of *Ostrya* parallels that of *Carpinus,* but the genus first appears somewhat later in the fossil record (Miocene), and fossils of *Ostrya* are not nearly so well represented (Crane). Although the disjunct populations of *Ostrya* in the mountains of Mexico have generally been considered to be conspecific with the species of the eastern United States (Miranda & Sharp; Nee), the same phytogeographic evidence cited in connection with Latin American *Carpinus* suggests that these populations may have been derived not from *O. virginiana,* but rather from an earlier and more western species.

Ostrya, like *Carpinus,* suffers from few insect pests or diseases, and none of these is regarded to be of economic importance. Sargent (1896) listed a number of insects that feed on or otherwise affect hornbeams. Hepting discussed various parasitic fungi, mostly found on *Ostrya* leaves.

The wood of *Ostrya* is employed for fuel, fence posts, and other utility purposes. It was formerly used for making items subject to prolonged friction, including sleigh runners, wagon tongues, wheel rims, spokes, windmill vanes, and airplane propellers. Because of its density, it has been used for tool handles, mallet heads, and other hard wooden objects. Millspaugh listed a tincture of the heartwood of *Ostrya virginiana* as a treatment for intermittent fever. *Ostrya virginiana,* and sometimes *O. carpinifolia,* are occasionally cultivated in eastern North America.

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Under family references see Abbe (1935, 1974); Candolle; Duncan; Hall; Hardin & Bell; Hepting; Koch; Lee (1973); Li & Cheng; MacDonald; Michaux; Miranda & Sharp; Radford; Rafinesque; Sargent (1896); Spach (1842b); and Winkler.

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Tribe Coryleae Meisner

5. **Corylus** Linnaeus, Sp. Pl. **2:** 998. 1753; Gen. Pl. ed. 5. 433. 1754.

Medium-sized to large shrubs [or small to medium-sized, usually spreading trees]; branching mostly deliquescent; trunks and branches terete, the branchlets and twigs subdistichous to diffuse; twigs differentiated into long and short shoots. Bark close, thin, smooth, grayish brown, breaking into vertical strips and scales with age, lenticels inconspicuous; young twigs glabrous or sparingly pubescent, sometimes with resinous glands; leaf scars suboval to triangular, with 3 nearly equidistant circular to elliptic vascular bundle scars; winter buds sessile, broadly ovoid, terete, divergent, the apices acute, with several smooth, imbricate scales; wood fine grained, nearly white to light brown, moderately hard, moderately heavy; pith circular to slightly angular in cross section. Leaves distichous, borne on long and short shoots; blades thin, broadly ovate, the base often cordate, occasionally somewhat lobed above, doubly serrate, usually pubescent and sometimes glandular abaxially; secondary venation craspedodromous, the lowest veins sometimes crowded at the base of the midrib and rising abruptly toward the apex; leaves in bud conduplicate and plicate; stipules broadly ovate. Staminate catkins lateral in bud axils on short shoots, in numerous racemose clusters of (2 or) 3–5, formed the previous growing season

and exposed during the winter, expanding long before the leaves, the scales broadly ovate, relatively uncrowded, consisting of 3 fused bracts; carpellate inflorescences lateral, borne near the tips of the branchlets producing staminate catkins, developing at the same time as the staminate, enclosed within buds during the winter and expanding long before the leaves, consisting of a small cluster of flowers and bracts, only the styles protruding from the buds at anthesis, the scales 3 fused bracts. Staminate flowers 3 per scale in the catkin, congested, the tepals lacking [(or 1–4)], the stamens 4, divided nearly or entirely to the base to form 8 half-stamens, the filaments very short, fused along with 2 bractlets to the scale; pollen grains flattened, 12–30 μm in diameter, slightly to moderately aspidote, with (2 or) 3 (or 4–6) slightly elliptic equatorial apertures. Carpellate flowers sessile, 2 per scale, with 4 extremely reduced tepals (displayed as a thin irregular fringe on the ovary); ovary 1, 2-locular, with 2 linear styles; ovule 1 by abortion, bitegmic. Infructescences consisting of compact clusters of several fruits, each subtended and surrounded by an involucre of 2 hairy [or spiny] expanded foliaceous bracts, these sometimes fused into a [short to] elongate tube. Fruits relatively thin-walled, subglobose to ovoid, somewhat laterally compressed, longitudinally ribbed nuts; pericarp bony; seed with membranaceous testa, the cotyledons thick and oily; germination hypogeal, the seed being raised to the surface but remaining in the fruit. Chromosome number $2n = 28$. LECTOTYPE SPECIES: *Corylus Avellana* L.; see N. L. Britton, N. Am. Trees, 246. 1908; N. L. Britton & A. Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **1**: 607. 1913. (The Latin name used by Virgil, Pliny, and other ancient writers for the European hop hornbeam; from *korus,* "helmet," for the shape of the shells of the nuts.)—HAZEL.

About 15 species of trees and shrubs of the North Temperate Zone. *Corylus Colurna* L., Turkish filbert or hazel, is a medium-sized tree of southeastern Europe and Asia Minor. The other species of Europe and North America are small to large shrubs or small trees. Two species, *C. americana* Walter, American hazel, and *C. cornuta* Marsh. (*C. rostrata* Aiton), beaked hazel, occur throughout much of the northeastern United States and adjacent Canada. In the Southeast these are mostly confined to the mountains southward to northern Alabama and Georgia. Several varieties of *C. cornuta,* including the tree-sized var. *californica* (A. DC.) Sharp, occur to the west.

Corylus was treated as a genus by Linnaeus and his predecessors. Spach (1842c) divided the genus into three sections, *Avellana* Spach (*C. Avellana* and *C. Colurna*), *Tubo-Avellana* Spach (*C. tubulosa* Willd. and *C. rostrata*), and *Acanthochlamnys* Spach (*C. ferox* Wall.). The second of these groups is characterized by an elongate tubular involucral beak, and the last by densely spiny bracts. De Candolle modified this scheme, making the first two groups subsections of sect. *Avellana.* Winkler recognized no infrageneric categories of *Corylus* in his monograph of the Betulaceae. In his synopsis, Beijerinck described 32 species, varieties, and cultivars of the genus. Lee (1973) listed 15 Chinese species, while Li & Cheng recognized seven. As in the other genera of the Betulaceae, the relatively poorly known Asian species need to be examined in relation to the genus as a whole. No infrageneric taxa are recognized here, pending detailed study of subgroups of the genus.

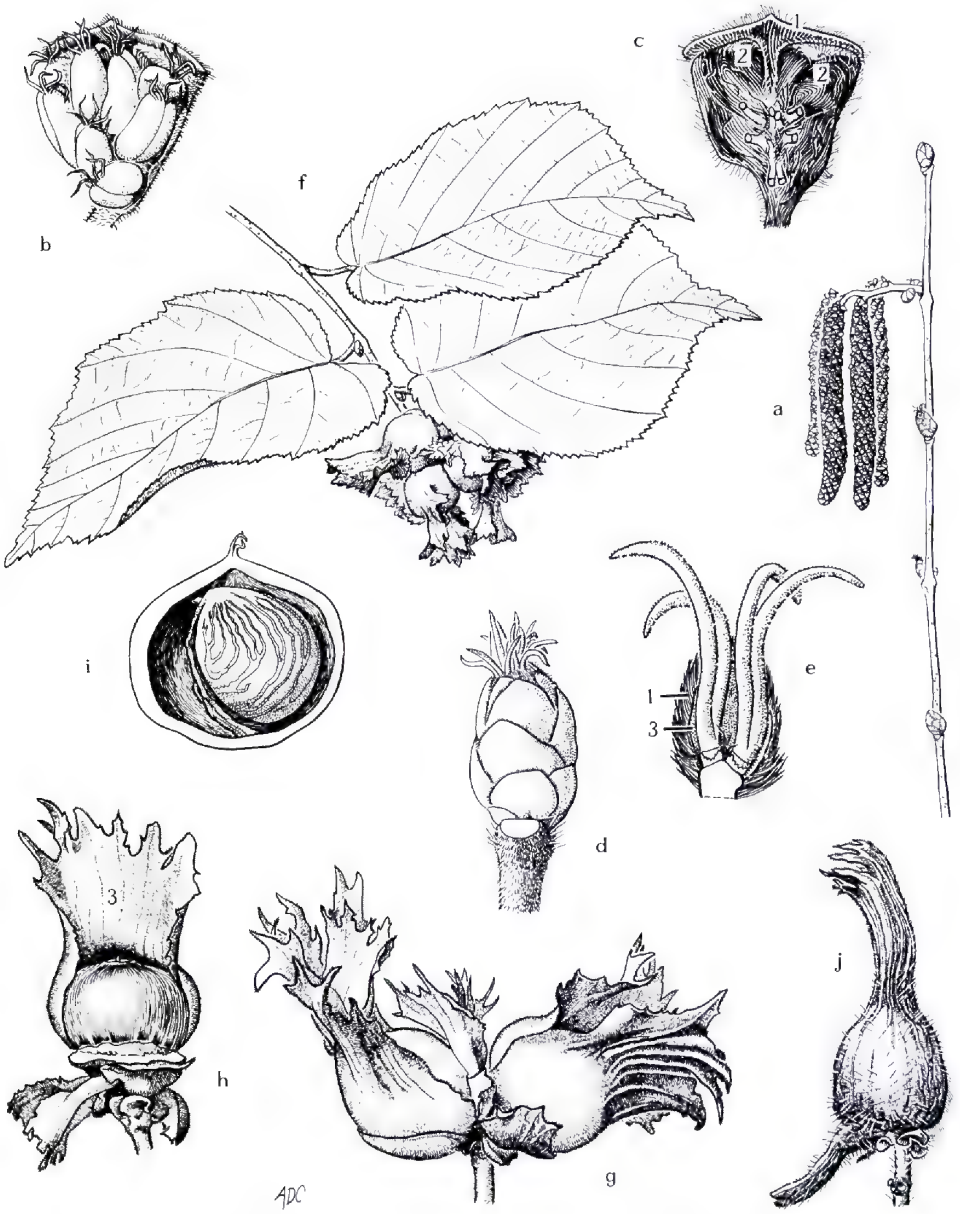

FIGURE 4. **Corylus.** a–i, *C. americana*: a, branchlet with flowering catkins, the 4 staminate ones pendent, the 3 carpellate ones ascending, the styles visible, ×½; b, adaxial side of staminate cymule with 8 half-anthers, primary bract and 1 secondary bract (at right) visible behind them, ×8; c, same, 8 half-anthers removed, bases of filaments shown, primary (1) and 2 secondary (2) bracts visible, ×8; d, carpellate catkin, ×4; e, adaxial side of carpellate cymule of 2 flowers, styles receptive, ovaries hardly developed, each ovary with delicate, rudimentary perianth, primary bract (1) and parts of tertiary bracts (3) visible behind flowers, secondary bracts absent, ×13; f, branchlet with 3 nearly mature fruits with their accrescent paired tertiary bracts, ×½; g, 2 mature fruits, each surrounded by tertiary bracts, ×1; h, mature nut with 1 tertiary bract (3) behind, the other removed, ×1; i, nut to show seed with half of pericarp removed at right and aborted ovule at upper left, ×2. j, *C. cornuta*: mature fruit with paired tertiary bracts and (at lower left) undeveloped fruits with bracts, ×1.

Corylus americana is a shrub to about 3 m tall, occurring mostly in thickets, open woods, fence rows, and forest edges, especially on well-drained soils, from Maine to Missouri and south to Georgia and Oklahoma. Its broadly ovate or roundish, doubly serrate leaves are distinctive in that they are often expanded apically to give a squarish appearance. *Corylus cornuta* is similar in habitat and distribution, but it extends farther north and west (from Newfoundland to British Columbia and south to Georgia, eastern Kansas, Colorado, and California). It is a larger plant than *C. americana,* reaching a height of about 5 m, and its leaves are narrower and more ovate. Drumke concluded that *C. cornuta* var. *californica* (A. DC.) Sharp, which becomes a small tree, is sufficiently distinct to warrant varietal status. He noted that this form grades clinally into var. *cornuta* to the north in Oregon and Washington. Useful field characters for separating the two species include the presence of reddish stipitate glands on the petioles and young twigs of *C. americana* and their absence on the petioles of *C. cornuta* (see Wiegand), and more rounded bud apices in *C. americana. Corylus cornuta* differs most noticeably from *C. americana* in the narrow, extended, tubular involucres surrounding its fruits, those of *C. americana* being short and leaflike. Drumke examined populations of these two species in their region of overlap and found them to be morphologically distinct, with little or no evidence of hybridization.

Although clearly related at the family level, the hazels are morphologically distinct both from the Betuloideae and from *Carpinus* and *Ostrya.* Their most distinctive features lie in their infructescences, which consist of a small cluster of small to moderately large nuts, each enclosed by a loose involucre of leaflike bracts. As in *Ostrya,* staminate catkins are formed during the summer and are exposed through the winter prior to anthesis. However, these are represented by numerous clusters of catkins borne on short shoots arranged evenly along the branches. The carpellate catkins develop at the same time as the staminate and consist of only a few flowers protected by the scales of special buds.

The leaves of *Corylus* resemble those of the other Betulaceae in overall aspect, but they are modified in shape and venation. As noted by L. J. Hickey & Wolfe and Wolfe (1973), the blades are frequently broader, and the lowest secondary veins, which are congested at the base of the midrib in some species, rise sharply toward the apex, a pattern also seen in *Corylopsis* of the Hamamelidaceae (see further discussion above under the family treatment). The indumentum on the leaves of *Corylus* is very similar to that of *Ostrya* and (to a slightly lesser degree) *Carpinus* (Hardin & Bell). All three genera lack peltate scales but have the five other trichome types described by Hardin & Bell. However, the stipitate glands of *Corylus* and *Ostrya* have multiseriate stalks, while those of *Carpinus* are more primitive in their uniseriate stalks (Hardin & Bell). The genus is the most specialized of the family in its fruit type (well-developed nuts) and the accompanying involucre (Stebbins; Stone).

Corylus stands apart from the remainder of the family in terms of flower and inflorescence morphology. The staminate inflorescences are similar in structure to those of the other Coryloideae except that up to four tepals are occasionally present, clearly defining the three individual flowers that make up each cymule. The carpellate catkins are much modified. The inflorescence itself

is reduced to a small cluster of flowers, only one or two of which develop further. Present in each partial inflorescence are two flowers, as in *Carpinus* and *Ostrya,* plus one primary and several additional bracts. Abbe (1935) interpreted the latter to represent various of the four tertiary bracts of a cymule (the secondary bracts not developing), but Hjelmqvist (1948) believed the two secondary bracts to be present, each fused to one of the two tertiary bracts associated with every flower (cf. Abbe, 1974). The two resulting foliaceous bracts grow around the developing fruit, either free from each other, as in *Corylus americana,* or fused into a tube, as in *C. cornuta* (see Abbe, 1974). Abbe (1974) reviewed the development of present concepts regarding the nature of the involucre of *Corylus* and various misconceptions that have involved its structure and development.

All investigated species of *Corylus* have chromosome numbers of $2n = 28$.

The inflorescences are produced the season before flowering, with the staminate being exposed during the winter and the carpellate enclosed in buds. Anthesis usually occurs extremely early (January or February), even in northern areas, and well before production of the new leaves. The plants are anemophilous, producing large quantities of pollen (Wodehouse, 1935). Dispersal is (apparently) by means of small mammals that carry the nuts away.

The wood of *Corylus,* like that of *Carpinus* and *Ostrya,* contains numerous small vessels with spiral secondary thickenings (Hall). However, its vessels, like those of *Alnus* and *Betula,* have scalariform perforation plates and are thus regarded as more primitive than those of the other Coryloideae (Hall). Hall concluded that true tracheids are absent from all of the Coryloideae, although fiber tracheids are present. However, Kasapligil (1964) and Yagmaie & Catling have reported tracheids in *Corylus* wood. Kasapligil (1964) noted two distinct subgroups of the genus on the basis of wood anatomy, with one, including *C. Avellana,* mostly lacking true tracheids and having fewer and wider bars in the perforation plates of its vessels, and a second, more primitive group (including *C. Colurna*) with wood composed of both tracheids and vessels, the latter with numerous narrow scalariform perforations. He suggested, on the basis of indumentum and other characters, that this second group might also include *C. ferox,* but that a formal assignment of *C. Colurna* to sect. *Acanthochlamnys* would require additional study. According to Hall, the wood of *Corylus* is anatomically indistinguishable from that of *Ostryopsis.*

Fossil leaves from the Late Cretaceous and early Paleocene have been identified as *Corylus,* but fossil fruits of the *Corylus* type are scarce during this period (Crane, 1981). A probable small *Corylus* nut was discovered in the Danian of Greenland by Koch. By the Pliocene, the genus had become well established in North America and Europe. Zoöchory, a novelty in the Betulaceae, has been regarded by both Stebbins and Stone as a specialized condition; all of the other genera (except *Ostryopsis*) rely on wind or water for dispersal. Crane (1981) pointed out that zoöchory is related to more stable K-selective environments than is anemochory, and its development may have paralleled the evolution of suitable animal dispersal vectors during the Paleocene, these permitting the genus to diversify into new niches.

Corylus is the source of hazelnuts and filberts. The commercial filbert (*C.*

Avellana and *C. maxima* Miller) and the Turkey nut (*C. Colurna*) are cultivated as crop plants in various parts of the world, particularly Turkey, Italy, Spain, China, and Japan. In the United States these species are grown commercially in the Pacific Northwest, where they produce over 10,000 metric tons of nuts annually, about five percent of the world crop (Schery). The fruits are used mostly as dessert nuts, but they are rich in oil (up to 68 percent) and serve as a commercial source for cooking and salad oil in Europe (Eckey; Vaughn). The kernels are sometimes ground into meal used to make a sweet, cakelike bread (Fernald *et al.*). Wild hazelnuts are gathered locally in both America and Europe. The pollen of hazels causes hay-fever allergies in regions where they occur in abundance (Dalen & Voorhorst; Lewis *et al.*; Løwenstein *et al.*; Wodehouse, 1945). The wood of the tree-sized species, which is similar in structure to that of birches, is used in limited amounts for pipe stems, hoops, tool handles, carved items, molding, and boxes. *Corylus cornuta* spreads aggressively and is considered a weedy pest in northern forest plantations (Tappeiner). Cultivars of a number of species, especially the shrubby *C. Avellana* and the arborescent *C. Colurna,* are widely planted as ornamental shrubs.

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THE GENERA OF TAXACEAE IN THE SOUTHEASTERN UNITED STATES[1]

ROBERT A. PRICE[2]

TAXACEAE S. F. Gray, Nat. Arr. Brit. Pl. **2:** 222. 1821, "Taxideae," nom. cons.

(YEW FAMILY)

Evergreen dioecious (or rarely monoecious) trees or shrubs. Foliage leaves entire, linear to linear-lanceolate, spirally arranged (often apparently 2-ranked) [or opposite in *Amentotaxus*], short-petiolate, with 2 stomatal bands on the abaxial surface; resin canal single, abaxial to the vascular bundle (or absent in *Taxus, Pseudotaxus,* and *Austrotaxus*). Wood without resin canals, axial wood parenchyma present or absent, helical thickenings present on the tracheid walls [apparently absent in *Austrotaxus*]. Pollen cones (microsporangiate strobili) apparently simple, borne singly in the axils of foliage leaves [or compound and

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible through the support of National Science Foundation Grant BSR-8716834 (Norton G. Miller, principal investigator), under which this account was prepared, and BSR-8717333 (Carroll E. Wood, Jr., principal investigator). The 131st in the series, this paper follows the format established in the first one (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. The references that I have not verified are marked with asterisks.

I thank Carroll Wood and Norton Miller for the opportunities afforded by participation in the Generic Flora Project and for their guidance in the study. I am grateful to Rudolf Schmid for bibliographic assistance, to Paul Groff for critical reading of the manuscript, and to Robert Godfrey for providing wild-collected material of *Taxus floridana,* on which the illustrations are based. The Center for Plant Conservation graciously provided photographs of *Torreya taxifolia.* Library and herbarium collections associated with Harvard University and the University of California, Berkeley, were consulted in this study, and I wish to thank the staffs of these institutions.

The illustrations were drawn by Linda Vorobik under the supervision of the author. The illustrations of *Torreya taxifolia* are based on living material from the University of California Botanical Garden, on seeds collected in Georgia by the staff of Callaway Gardens, and on *W. F. Jacobs 8528* (UC) and *R. K. Godfrey 55449* (UC). The longitudinal and cross sections of the seed of *Torreya* are redrawn from photographs in Coulter & Land, while the arillate seed of *Taxus floridana* was redrawn from an original illustration supplied by Robert Godfrey.

Contribution 616 from the New York State Science Service.

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Journal of the Arnold Arboretum **71:** 69–91. January, 1990.

aggregated in *Amentotaxus* and *Austrotaxus*]; microsporophylls several per strobilus, more or less whorled, each with [2 or] 3–9 microsporangia borne in a radial arrangement (*Taxus, Pseudotaxus*) or developing fully only on the abaxial side (*Torreya, Amentotaxus*); pollen grains nonsaccate, lacking prothallial cells. Ovules arillate, borne singly at the ends of short axillary shoots[3] bearing decussate [or spirally arranged] scale leaves; archegonia usually few per ovule, not clustered. Seeds with a stony coat, largely surrounded by the fleshy aril; embryo straight, cotyledons 2 (or occasionally 1 or 3). Chromosome number $2n = 22$ or 24 [14 in *Amentotaxus*]. (Including Amentotaxaceae Kudo & Yamamoto, Austrotaxaceae Nakai, Torreyaceae Nakai; Taxineae L. & A. Richard.) TYPE GENUS: *Taxus* L.

A small family of five genera and perhaps 20 species, the Taxaceae are widely distributed in the Northern Hemisphere in moist, forested habitats from the subarctic of Eurasia and North America to subtropical or even tropical areas of Central America and southeastern Asia. The monotypic *Austrotaxus* Compton is endemic to New Caledonia, while *Taxus* L. ranges south of the equator on Sumatra and Celebes (Florin, 1963). Only the two most widespread genera, *Torreya* Arnott and *Taxus,* occur in North America, including the southeastern United States. The monotypic *Pseudotaxus* Cheng (*Nothotaxus* Florin) is endemic to eastern China, while *Amentotaxus* Pilger has four species in southeastern Asia, occurring from central and southern China, including Taiwan and Hongkong, to southern Vietnam and extreme eastern India (Alvin *et al.*; Ferguson, 1985; Florin, 1963). *Amentotaxus* is also known from fossils of Tertiary age in western North America and Europe, but it had disappeared from these areas by the Late Miocene or Early Pliocene (Alvin *et al.*; Florin, 1963).

The Taxaceae, both fossil and extant, are unique among the conifers in having arillate ovules borne singly at the ends of lateral short shoots, but with no evidence of a biaxial ovulate cone or ovuliferous scales. Thus Florin (1938–1945, 1948a) proposed that they form an evolutionary lineage separate from the conifers. However, the Taxaceae have the specialized pattern of proembryogeny typical of the modern conifers (Dogra; Doyle, 1963), and they share derived features of wood anatomy and pollen and leaf morphology with other modern families of conifers, particularly the Cephalotaxaceae, a monogeneric family native to eastern Asia. On the bases of overall similarity and preliminary phylogenetic analyses (Hart), it seems most likely that the Taxaceae are conifers, most closely related to *Cephalotaxus* Sieb. & Zucc. ex Endl., that have secondarily lost the coniferous ovulate cone organization, although there are no intermediates indicating how the ovules have come to be terminal in position.

Cephalotaxus (plum-yew, with nine species in Fu's treatment) is very similar to the Taxaceae in appearance and in a number of morphological features. It differs most prominently from the Taxaceae in having its young ovules borne

[3]In *Taxus* and *Torreya* the ovule-bearing short shoots are axillary to scale leaves borne on very short axillary shoots, while in the other genera they arise from the axils of foliage leaves (Florin, 1948a). In *Torreya* there are usually two ovuliferous shoots on each dwarf axillary shoot, but only one ovule generally matures.

in pairs along a cone axis. Each pair of ovules is subtended by a bract and is associated with a small outgrowth that has been interpreted as an extremely reduced ovuliferous scale (Florin, 1951; Singh, 1961). Generally only one or two ovules mature per cone. The ovular integument differentiates into an inner stony layer and an outer fleshy layer, making the seed similar in structure and appearance to those of *Torreya* and *Amentotaxus,* but there is no evidence of a separate aril in the development of the ovule (Singh, 1961).

Until the early 1900's the Taxaceae were often treated as including both the Cephalotaxaceae and the Podocarpaceae (Pilger, 1903, 1916b), primarily on the grounds that these groups have fleshy structures surrounding the seed and often have the ovuliferous scales greatly reduced. The Podocarpaceae are very diverse in their ovulate-cone morphology. Cones of some species are highly reduced and bear only a single ovule, while the more primitive members of the family have prominently biaxial ones with a number of ovules (Quinn; Sporne). The Podocarpaceae have a unique binucleate cellular stage in their early embryogeny, and all but two of the genera have an epimatium (an unusual structure generally interpreted as a modified ovuliferous scale that partially folds around the ovule) as the fleshy structure associated with the seed (Florin, 1958b; Quinn). The aril surrounding the seed of the Taxaceae arises as an outgrowth at or just below the base of the ovular integument (Coulter & Land; Keng; Loze). Elsewhere among the conifers, a comparable structure occurs only in the podocarpaceous genus *Phyllocladus* L. & A. Rich. (Sporne), a highly derived group otherwise very dissimilar from the Taxaceae. The Taxaceae and Podocarpaceae also differ in wood anatomy, pollen structure, and chemistry, and there is thus little evidence of a close relationship between the two families (see Florin, 1958b; Hegnauer, 1962, 1986; Phillips).

Two tribes are often recognized in the Taxaceae, following the treatment of Janchen. In plants of tribe Torreyeae Janchen, including *Torreya* and *Amentotaxus,* the microsporangia are borne abaxially on the microsporophylls (vs. radially arranged in tribe Taxeae) and the aril tightly invests the mature seed and is largely adnate to the seed coat (Florin, 1948a; Keng). In these two genera the free portion of the aril is displaced toward the apex of the ovule by intercalary growth, while in the three genera of tribe Taxeae (*Taxus, Pseudotaxus,* and *Austrotaxus*) the entire aril remains free from the ovular integument and forms a cuplike structure around the seed (Florin, 1948a). The genera of tribe Taxeae also lack the foliar resin canal present in *Torreya, Amentotaxus,* and the outgroup *Cephalotaxus* (Gaussen). *Austrotaxus* is unique in the family in having the microsporangia partially connate (Saxton; Wilde) and in apparently lacking helical thickenings on the tracheid walls (Greguss, 1955; Phillips). It has recently been found, however, to produce taxane alkaloids, which had previously been known only from *Taxus* (Guéritte-Voegelein *et al.*).

Chromosome numbers have been reported for three of the genera of Taxaceae. Counts of $2n = 24$ have been obtained for four species of *Taxus* (Dark; Sax & Sax; Sugihara, 1946b). This is presumably the primitive chromosome number for the family, since it has also been obtained for several species of the outgroup genus *Cephalotaxus* and is apparently the primitive number for the conifers generally (Ehrendorfer; Khoshoo, 1961, 1962). Eleven of the chro-

mosomes in *Taxus* are metacentric or submetacentric, while the shortest one is subtelocentric (Dark; Sax & Sax).

The chromosome number $2n = 22$ has been obtained from two species of *Torreya, T. nucifera* (L.) Sieb. & Zucc. (see, for example, Tahara, Terasaka) and *T. californica* Torrey (see Gaussen). All of the chromosomes of *T. nucifera* are apparently metacentric or submetacentric (Terasaka). The count of $2n = 22$ has also been reported for *Amentotaxus argotaenia* (Hance) Pilger by Sugihara (1946a), but his illustration is unclear. In contrast, Chuang & Hu provided an excellent illustration of the chromosomes of *A. formosana* Li (as *A. argotaenia*), with $2n = 14$, equaling the lowest chromosome number known for any gymnosperm (see Khoshoo, 1961). All of the chromosomes in this species are clearly heterobrachial, and two are markedly shorter than the rest (Chuang & Hu). Counts for other populations of *Amentotaxus* and for *Austrotaxus* and *Pseudotaxus,* as yet unstudied, are much needed.

The proembryogeny of the Taxaceae is similar to that of other groups of conifers, including *Cephalotaxus* and members of the Podocarpaceae (see reviews in Dogra; Doyle, 1963; Doyle & Brennan; Singh, 1978). After cell walls are formed, there is a single upper tier of cells that are open at the top, with an irregularly storied group of cells below. There is a trend among the gymnosperms toward reduction in the number of free-nuclear mitotic divisions in the proembryo prior to cell wall formation. Eight sets of free-nuclear mitoses are found in *Ginkgo,* and there are still higher numbers in the cycads, while six sets or fewer occur in the conifers (Dogra; Singh, 1978). There are usually four sets of free-nuclear mitoses in *Cephalotaxus, Taxus, Pseudotaxus, Amentotaxus,* and *Austrotaxus* (Buchholz, 1940; Chen & Wang, 1978, 1984a, b; Saxton; Singh, 1961, 1978; Sterling, 1948; Sugihara, 1946a, b), while in *Torreya* the number of such divisions has been reduced to two or three sets, yielding a four- or eight-celled proembryo (see review in Doyle & Brennan). Each of these genera frequently exhibits simple polyembryony. Cleavage polyembryony has been documented in *Torreya* (Chen & Wang, 1984a; Doyle & Brennan), but not in the other genera of Taxaceae and only as a rare event in species of *Cephalotaxus* (Singh, 1961).

The microsporangiate strobili of the Taxaceae are diverse in structure and have been the subject of varied morphological interpretations (see, for example, Florin, 1948a; Sporne; Wilde). In *Amentotaxus* the strobili are compound structures with some 20 to 30 small strobilar units arranged in a more or less decussate fashion along the axis (Keng; Wilde). The outgroup *Cephalotaxus* also has compound microsporangiate branches, with each lateral strobilus in the axil of a bract, indicating that a compound strobilus may be primitive in the Taxaceae (Wilde). No bracts are evident subtending the lateral units in *Amentotaxus,* each of which bears eight to 12 microsporophylls in *A. argotaenia. Austrotaxus* also has an unusual spikelike strobilar structure, in which the very reduced sporangia-bearing structures occur in the axils of spirally arranged bracts along the cone axis. Based on the pattern of vasculature, Wilde has interpreted the axillary structures as highly reduced lateral cones in which the sporophyll stalks are virtually absent and the sporophylls and sporangia are partially fused. *Pseudotaxus* seemingly has simple pollen cones in the axils

of foliage leaves, but two scale leaves are positioned on the axis between whorls of sporophylls (Florin, 1948b; Wilde), possibly indicating reduction from a more complex structure. *Taxus* has pollen cones rather similar to those of *Pseudotaxus* (but lacking sterile scales between the sporophylls), while *Torreya* has simple axillary pollen cones without sterile scales.

The radial arrangement of microsporangia in *Taxus* and *Pseudotaxus* is very unusual among the conifers and is somewhat reminiscent of the arrangement of sporangia in *Equisetum* L. (Sporne). Radially arranged microsporangia are also sometimes found at the apices of strobili in *Cephalotaxus* and *Amentotaxus,* in which the sporangia are usually fully developed only on the abaxial surface (Wilde). By analogy, Wilde has thus suggested that the sporangia-bearing structures of *Taxus* and *Pseudotaxus* may be equivalent to reduced lateral cones. In *Torreya,* however, the sporangial initials are radially arranged, and those on the adaxial side abort early in development to give the asymmetric arrangement seen at maturity (Coulter & Land).

The bark of *Taxus* and *Torreya* is unusual in having fibers with prominent crystals of calcium oxalate on the outer cell walls (Chang; Lotova). Crystalliferous fibers apparently are also present in *Amentotaxus* but are absent in *Austrotaxus* and in the outgroup *Cephalotaxus* (Outer & Toes).

Resin canals are absent in both the bark and the wood of Taxaceae and Cephalotaxaceae (Chang; Phillips; Suzuki, 1979a), although they are present in the leaves and arils of *Torreya* and *Amentotaxus,* as well as in the leaves and fleshy seed coat of *Cephalotaxus* (Keng; Singh, 1961). Individual resiniferous parenchyma cells are apparently present in the wood of *Cephalotaxus* (Greguss, 1972) and also in that of *Torreya* (Bliss), in accord with the distinctive odor of the wood in several species of the latter. Resiniferous parenchyma cells are evidently absent from the stem wood of *Taxus* but may be present in the root wood (Bliss).

Helical thickenings on the secondary walls of the axial tracheids are a notable feature of the wood in Taxaceae and *Cephalotaxus* (Greguss, 1955; Penhallow; Phillips). Apparently they are usually absent in *Austrotaxus* (Gaussen; Greguss, 1955), although according to Phillips they were reported for this genus by Prince. The form and distribution of helical thickenings on the tracheids of Taxaceae are strikingly similar to those of *Cephalotaxus* but differ from those found in some of the Pinaceae (Penhallow; Yoshizawa *et al.*).

Leaf anatomy has proved particularly useful in differentiating the genera of Taxaceae (Ferguson, 1978; Florin, 1931, 1948b, 1951) and has often allowed unequivocal identification of fossil leaves. *Amentotaxus* is notable for the starlike arrangement of subsidiary cells around the guard cells, with some of the subsidiary cells shared by adjacent stomata. The outer surface of the subsidiary cells is prominently thickened and papillate in *Taxus* but unthickened in *Pseudotaxus.* The stomata are monocyclic in *Torreya* and *Amentotaxus* and are usually so in *Pseudotaxus,* while they are amphicyclic in *Taxus* and *Austrotaxus.*

The pollen grains of Taxaceae are nonsaccate and lack prothallial cells, as is also the case in the Cephalotaxaceae, Sciadopityaceae, and Cupressaceae (including Taxodiaceae) (Erdtman, 1957, 1965; Singh, 1961, 1978; Ueno, 1959, 1960; Wodehouse). Presence of pollen saccae (as in most Pinaceae and Po-

docarpaceae and several extinct groups of conifers) and two prothallial cells (as in Pinaceae and *Ginkgo,* with secondarily higher numbers in Araucariaceae and most Podocarpaceae) are apparently the primitive states among the conifers (see Florin, 1951; Millay & Taylor; Singh, 1978). The sculpture and structure of the pollen grains of the Taxaceae are similar in general features to those of the Cephalotaxaceae and Cupressaceae (Owens & Simpson; Ueno, 1959), although unique features have recently been ascribed to *Amentotaxus* (Xi, 1986a, b). The Taxaceae are wind pollinated, as are virtually all gymnosperms, and have a pollination-drop mechanism of pollen capture, as is the case in *Ginkgo* and a number of groups of conifers, including the Cephalotaxaceae and Cupressaceae (Doyle, 1945; Singh, 1978).

The Taxaceae are one of several gymnospermous groups in which dioecy is coupled with a seed-dispersal syndrome involving mammals or birds as vectors (Givnish). *Taxus* exhibits a typical pattern of characters related to bird dispersal, with the attracting aril becoming sweet and red when the seeds ripen, while the seed itself is toxic and protected by a hard coat. The large, edible seeds of *Torreya,* with their dull purplish, resinous aril, are well suited to mammal dispersal. The seeds of *Torreya taxifolia* are highly sought after by squirrels (U. S. Fish & Wildlife Service). Field studies are needed to determine the dispersal mechanisms in the other genera, although preliminary morphological and chemical data tend to suggest bird dispersal in the other two genera of Taxeae.

Studies of the natural-product chemistry of the Taxaceae have been largely restricted to the genera *Taxus* and *Torreya,* with the exception of preliminary studies of the biflavonoid composition of *Amentotaxus* and *Pseudotaxus* (see reviews in Geiger & Quinn, 1975, 1982; Hegnauer, 1986) and of a few of the compounds extractable from the wood of *Pseudotaxus Chienii* (Cheng) Cheng (Ma *et al.,* 1982) and the leaves of *Amentotaxus argotaenia* (Ma *et al.,* 1986). What is known of the chemistry of the Taxaceae does not provide evidence favoring its treatment as a group separate from the other families of conifers (Hegnauer, 1962, 1986).

Only the amentoflavone series of biflavonoids appears to be present in the Taxaceae and Cephalotaxaceae, in contrast to the much greater diversity of biflavonoid structures found in the Araucariaceae, Cupressaceae (including Taxodiaceae), and Podocarpaceae (Geiger & Quinn, 1975; Hegnauer, 1962, 1986). Kayaflavone, the sole biflavonoid reported from four species of *Torreya* (see Geiger & Quinn, 1975; He *et al.,* 1983; Ma *et al.,* 1985), has not been found in *Amentotaxus, Pseudotaxus,* or *Taxus,* while the parent compound amentoflavone is the only biflavonoid reported to date from *Amentotaxus.* Mono-, di-, and trimethyl ethers of the series, including sciadopitysin, ginkgetin, and sequoiaflavone have been isolated from *Taxus baccata* (M. S. Y. Khan *et al.*; Morelli), while only sciadopitysin was reported from several other species of *Taxus* by Ma and colleagues (1985).

Leaf oils have apparently been investigated only in *Torreya,* in large part because foliar resin canals are absent in the other genera except for *Amentotaxus.* The major monoterpene components of *Torreya* leaf resin, including limonene, α-pinene, and myrcene, are also of wide occurrence elsewhere among

the conifers (He *et al.*, 1986; Hegnauer, 1962, 1986; Yatagai & Sato). A series of more unusual resin sesquiterpenes has also been isolated from the stem wood of *Torreya nucifera* (see reviews by Burke; Hegnauer, 1986), but only limited comparative studies have been conducted within the genus.

Taxus is notable for the highly poisonous taxane alkaloids, an unusual class of diterpene alkaloids that is characteristic of its leaves, stems, and seeds (Lythgoe; R. W. Miller). Some of these alkaloids, most notably taxol, have been the subject of considerable interest because of their potent antimitotic activity and potential utility as anticancer chemotherapeutic agents (Guéritte-Voegelein *et al.*; R. W. Miller). Taxane alkaloids had been considered to be unique to *Taxus* (Hegnauer, 1986, 1988) but have recently also been found to occur in *Austrotaxus* (Guéritte-Voegelein *et al.*). They are not present in *Torreya* but need to be thoroughly sought after in *Pseudotaxus*. A biosynthetically unrelated class of cytotoxic alkaloids is characteristic of *Cephalotaxus*, and these compounds are also under investigation for their anticancer activity (Chu; Huang & Xue). Alkaloids are of quite restricted distribution among conifers outside of the Taxaceae and Cephalotaxaceae, having been found only in a few members of the Pinaceae and in *Athrotaxis* D. Don (Cupressaceae *sensu lato*) (Hegnauer, 1988).

Taxus, which is widely grown as an ornamental hedge or tree in North America and Europe, is the only genus of Taxaceae with major economic importance. *Torreya* is of lesser importance as an ornamental, but it is valued in Asia for its wood, edible seeds, and seed oil. *Amentotaxus* and *Pseudotaxus* are of potential horticultural interest, but only *A. argotaenia* has been introduced into cultivation outside of China (Rushforth).

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KEY TO THE GENERA OF TAXACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *dioecious (rarely monoecious) evergreen shrubs or trees; foliage leaves alternate, appearing 2-ranked [or less commonly opposite], linear to linear-lanceolate, short-petiolate; pollen cones with whorled or tightly clustered microsporophylls; each sporophyll with [2 or] 3–9 abaxial or radially arranged microsporangia; pollen nonsaccate, lacking prothallial cells; ovules borne singly, terminating short axillary shoots; seeds arillate, with hard coat; cotyledons 2 (rarely 1 or 3).*

A. Seed ca. 2–5 cm long, completely surrounded by a greenish or purplish aril; leaves sharply pointed, aromatic when bruised, with a resin canal. ..... 1. *Torreya.*

A. Seed < 1 cm long, partially enclosed by a cup-shaped red aril; leaves not sharply pointed or strongly aromatic, without a resin canal. ..... 2. *Taxus.*

Tribe TORREYEAE Janchen

1. **Torreya** Arnott, Ann. Nat. Hist. **1**: 130. 1838, nom. cons.

Evergreen dioecious (rarely monoecious) trees with branches seemingly in whorls. Bark fissured. Wood with little or no axial parenchyma, persistently aromatic. Foliage leaves spirally arranged (appearing 2-ranked due to twisting of the leaf bases), linear to linear-lanceolate, sharply pointed at apex, strongly aromatic when bruised [or slightly so in *T. grandis*]; abaxial surface with 2 narrow, whitened [or sometimes brownish] stomatal bands with sunken stomata; resin canal single, abaxial to the vascular bundle. Pollen cones short-stalked, borne singly in leaf axils of the current year; microsporophylls in ca. 6–8 whorls of 4 per strobilus, distal to a series of tightly clustered decussate scale leaves; sporangia abaxial, usually 3–5 per sporophyll. Ovules borne singly, terminating short secondary lateral shoots, generally with 2 such ovuliferous shoots borne in the axils of scale leaves on a primary dwarf shoot axillary to a foliage leaf, usually only 1 ovule maturing per associated foliage leaf. Seeds ca. 2–5 cm long, surrounded by the resinous greenish or purplish aril, maturing the second year; seed coat heavily sclerified, adnate to the surrounding aril except at the distal tip; gametophytic storage tissue irregularly channeled ("ruminate"); embryo distal, very small when seed is shed. Chromosome number $2n = 22$. (*Tumion* Raf.) TYPE SPECIES: *Torreya taxifolia* Arnott. (After John Torrey, 1796–1875, noted American botanist.)—TORREYA, STINKING CEDAR.

A genus of seven species in moist temperate areas of eastern Asia and North America, with two native to the United States (*Torreya californica* Torrey in California and *T. taxifolia* Arnott in Florida and adjacent Georgia), one to Japan (*T. nucifera* (L.) Sieb. & Zucc.), and four to central and southern China (see the recent treatment in Cheng & Fu) and adjacent Burma (Florin, 1963). *Torreya* had a more extensive Northern Hemisphere range during Mesozoic and Tertiary times. The oldest fossils of the genus, from Great Britain and southern Scandinavia, are of middle Jurassic age, and the genus persisted in central and southern Europe until the Pliocene (Florin, 1958a, 1963).

Torreya most closely resembles *Amentotaxus* (and *Cephalotaxus*) in having large, drupelike seeds and elongate leaves with a single resin canal. *Torreya* differs from these genera and the remainder of the Taxaceae in having narrower stomatal bands with sunken stomata on the abaxial leaf surface (Ferguson, 1978; Florin, 1931), a pungent aromatic odor when its foliage is bruised, simple rather than compound microsporangiate strobili, and highly channeled ("ruminate") gametophytic storage tissue in its seeds. The last feature is unique among the gymnosperms and is caused by the irregular growth of megagametophytic tissue into the surrounding nucellar and integumentary tissues (Coulter & Land). It has given rise to the name "California nutmeg" for *Torreya californica*.

Torreya is apparently not divisible into clearcut infrageneric groups supported by multiple characters but has been divided into sect. NUCIFERAE Hu, with only slightly channeled seed-storage tissue (*T. nucifera* and *T. grandis* Fortune only), and sect. TORREYA (sect. *Ruminatae* Hu), with prominent channeling of the seed tissue (Cheng & Fu).

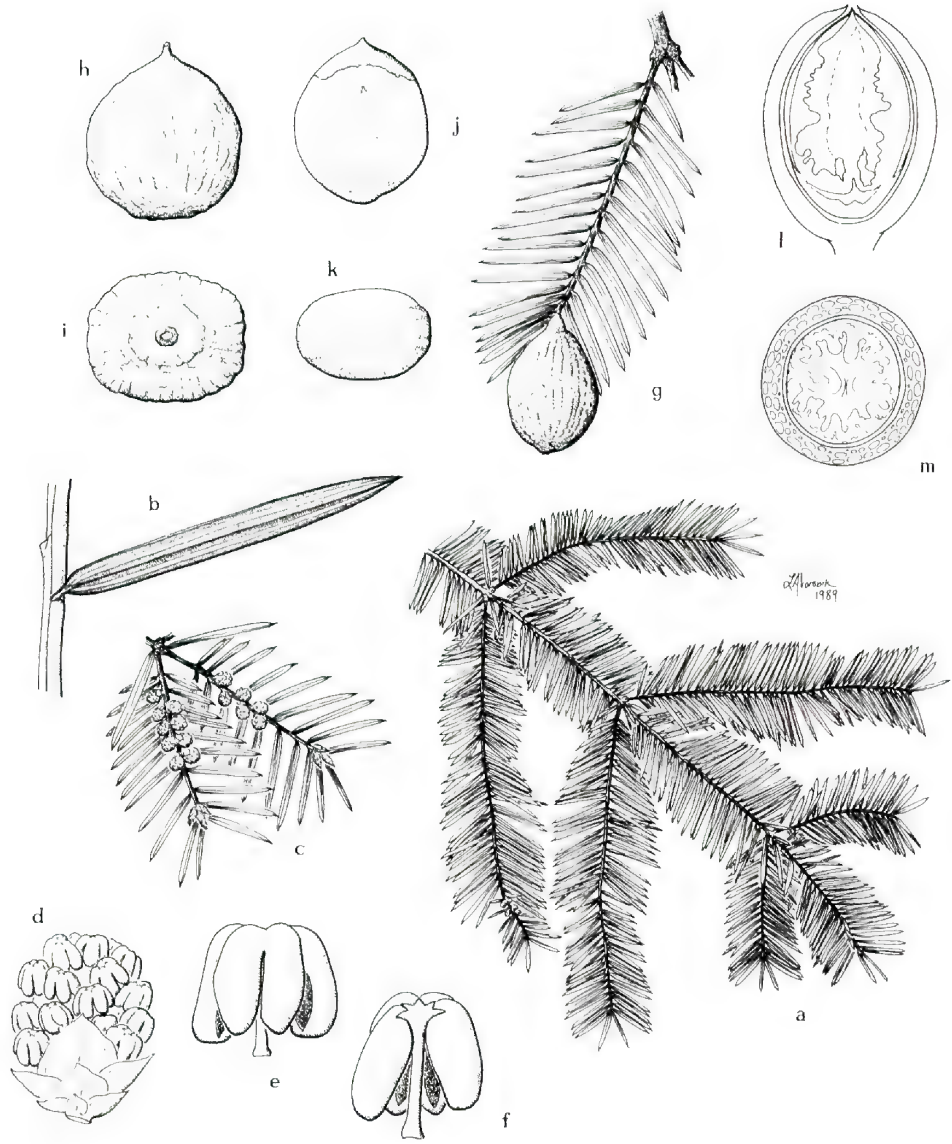

FIGURE 1. Tribe Torreyeae. a–m, *Torreya taxifolia*: a, leafy shoot, × ⅓; b, detail of leaf in abaxial view, × 1½; c, shoots bearing microsporangiate strobili, × ½; d, detail of microsporangiate strobilus with subtending bracts, × 5; e, f, microsporophyll in abaxial and adaxial views, × 20; g, shoot bearing mature seed, × ½; h, i, dry seed with aril, longitudinal and radial views, × ½; j, k, seed with aril removed, longitudinal and radial views, × ½; l, longitudinal section of mature seed showing "ruminate" gametophytic tissue, × ¾; m, cross section of moist arillate seed, showing resin canals in the aril and "ruminate" gametophytic tissue, × ¾.

Our sole species, *Torreya taxifolia* Arnott (*Tumion taxifolium* (Arnott) Greene), Florida torreya, stinking cedar, gopherwood, is a very narrow endemic restricted to moist, wooded slopes and limestone bluffs in the vicinity of the Apalachicola River in three counties (Gadsden, Liberty, Jackson) of north-

western Florida and in adjacent Decatur County, Georgia (Kral; Little, 1978; Stalter & Dial). The species was already significantly diminished in population size by the early 1900's because of cutting for lumber and fenceposts (Britton; Coulter & Land) and is now critically endangered because of the effects of a fungal blight. It is a listed endangered species at both the state and federal levels (U. S. Fish & Wildlife Service). At some point between 1954 and 1962, fungal disease(s) of the leaves and stems began to attack the native populations (Godfrey & Kurz). Several fungal pathogens have been isolated from diseased trees (Alfieri *et al.*; U. S. Fish & Wildlife Service), but the causative agent is still unknown. Drought and habitat degradation may have played a significant role in making the wild trees less resistant to fungal attack (Savage; Stalter & Dial). By 1981, essentially all wild individuals had been infected and all of the wild trees over 3 m tall had died back except for stump sprouting (Stalter & Dial). Only approximately 100 wild individuals were alive as of 1981. Further propagation of cultivated trees outside the native range will be needed to avoid the extinction of the species.

Torreya taxifolia differs from the other North American species, *T. californica,* in having yellowish brown rather than reddish brown second-year twigs and generally shorter leaves (2.5–4 cm vs. 3–8 cm) that are less flat on the adaxial surface. The stomatal bands are also less deeply sunken into the leaf in *T. taxifolia* than in *T. californica* and the other species of the genus (Krüssmann). The two species also evidently differ in their volatile oil chemistry, as indicated by differences in the odor of the bruised stems and foliage, described as pungently aromatic in *T. californica* and foul-smelling in *T. taxifolia* (Krüssmann; Sargent).

No systematic investigation of crossability in *Torreya* has been conducted. An apparently spontaneous hybrid of *T. californica* and *T. nucifera* was mentioned by Krüssmann.

The various species of *Torreya* are attractive ornamentals in cultivation. *Torreya californica* is the hardiest and most widely cultivated species of the genus in North America and Great Britain, while *T. nucifera* and *T. grandis* are grown primarily in their native countries in Asia, where several cultivars have been selected (Bean; Krüssmann). The large seeds of several species are highly esteemed food items. Seeds of *T. californica* were gathered by a number of tribes of native Americans, while those of *T. nucifera* are both eaten and used as a commercial source of cooking oil in eastern Asia (Burke). The very durable wood of *Torreya* has been valued for furniture, cabinetry, and fence posts (Burke; Dallimore & Jackson), and thus few large trees remain outside of cultivation.

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Tribe TAXEAE

2. **Taxus** Linnaeus, Sp. Pl. **2:** 1040. 1753; Gen. Pl. ed. 5. 462. 1754.

Dioecious (rarely monoecious) shrubs or trees. Bark reddish brown, becoming scaly with age. Wood without axial parenchyma. Foliage leaves spirally arranged (often appearing 2-ranked), linear, with 2 yellowish or grayish, abaxial stomatal bands; resin canals absent. Pollen cones short-stalked, borne singly in axils of foliage leaves; microsporophylls densely clustered, ca. 5–15 per strobilus, each with 4–9 radially arranged sporangia. Ovules borne singly in the axils of foliage leaves, each terminating an ovuliferous dwarf shoot borne laterally on a very short vegetative shoot in the axil of the foliage leaf. Seeds ca. 0.5[–1] cm long, largely surrounded by the cuplike reddish [rarely yellow] aril, which is not adnate to the highly sclerified seed coat; cotyledons 2 (rarely 3). Chromosome number $2n = 24$. LECTOTYPE SPECIES: *Taxus baccata* L.[4] (Classical Latin name for yew.)—YEW.

A genus of perhaps eight or nine poorly differentiated allopatric taxa, treated most often as separate species but sometimes as geographic subspecies (Pilger, 1903, 1926). The species of *Taxus* are very difficult to distinguish by either gross morphology or leaf anatomy (Florin, 1931; Kwei & Hu; Pilger, 1903). A thorough revision making use of comparative biochemistry as well as morphology is much needed. Four species are native to North America, of which two, *T. canadensis* Marsh. and *T. floridana* Chapman, occur in our region. *Taxus brevifolia* Nutt. is widely distributed but relatively uncommon in the extreme western United States and Canada, while the poorly known *T. globosa* Schlecht. is endemic to Mexico and Guatemala. *Taxus baccata* L. (English yew, Irish yew) is native to Europe, Asia Minor, and north Africa, while *T. cuspidata* Sieb. & Zucc. (Japanese yew) and two or three other species are native to eastern Asia and the Himalayas (Cheng & Fu; De Laubenfels, 1988). Given the fact that the genus apparently dates back to the Jurassic (Florin, 1958a; Harris, 1976b), it is remarkable how little morphological differentiation is seen among its extant members.

Taxus canadensis (*T. baccata* subsp. *canadensis* (Marsh.) Pilger; *T. baccata* var. *canadensis* (Marsh.) A. Gray, 1856; *T. baccata* var. *minor* Michx., 1803; *T. minor* (Michx.) Britton), Canada yew, American yew, ground hemlock, $2n = 24$, is native to an area extending from Newfoundland to Manitoba, south to portions of Iowa, Illinois, Indiana, eastern Kentucky, Virginia, and extreme northern Tennessee and North Carolina. It is usually found under cool, moist conditions on well-drained soil as an understory plant in coniferous or mixed-mesophytic forest. In the southern part of its range, it almost always occurs on upland sites. In our area it has only recently been found in Pickett County, Tennessee, on protected northern slopes on the western edge of the Cumberland Plateau (Gonsoulin) and under montane forest conditions in Ashe and Watauga

[4]The genus was effectively lectotypified by Siebold & Zuccarini, Fl. Japon. Fam. Nat. **2:** 108. 1846, when they transferred the only other Linnaean species, *Taxus nucifera,* to the newly described genus *Torreya.*

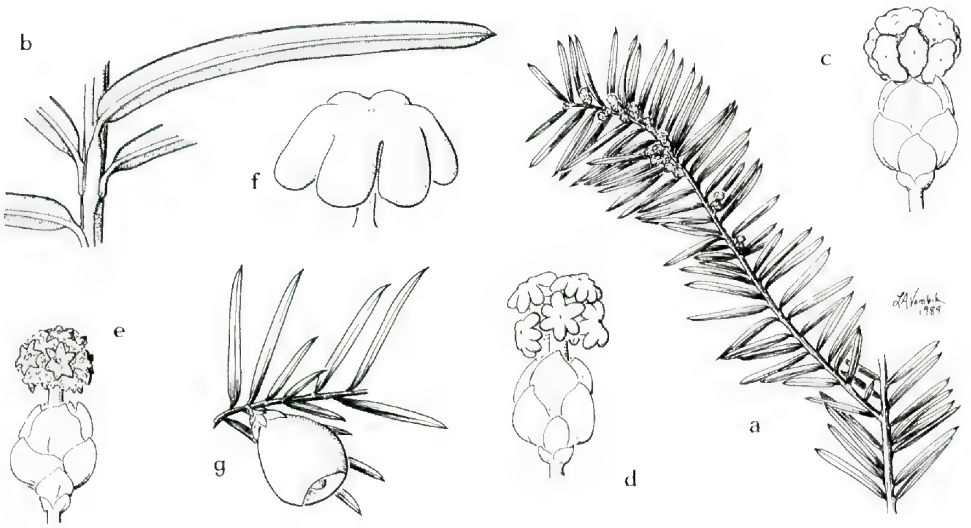

FIGURE 2. Tribe Taxeae. a–g, *Taxus floridana*: a, leafy shoot with microsporangiate strobili at time of pollen release, × ½; b, detail of leaf in abaxial view, × 2½; c, d, e, microsporangiate strobili before, during, and after shedding of pollen, × 5; f, detail of microsporophyll, × 20; g, shoot with arillate ovule, × 1⅕.

counties in extreme northwestern North Carolina (McDowell). Despite the fact that the foliage of the plant is toxic to most animals, Canada yew is a favored browse plant of deer and has been greatly reduced in numbers in much of the northeastern United States by the large resident deer populations (Martell).

Taxus floridana Chapman, Florida yew, savin, is a very rare species native only to areas of Gadsden and Liberty counties in northwestern Florida, largely in the vicinity of the Apalachicola River in the same area where *Torreya taxifolia* is native (Little, 1978). It occurs primarily on moist ravine slopes and sometimes bluffs in mixed deciduous forest, although one population has been found in an acidic bog (Kurz).

Taxus canadensis is usually a low shrub, occasionally becoming 2–3 m tall, while *T. floridana* is a small tree up to 10 m in height. The leaves of *T. canadensis* are yellowish green above, relatively flat, and ca. 1.3–2 cm long, while those of *T. floridana* are dark green above, usually falcate, and ca. 2–2.5 cm long (Rehder, 1940; Sargent). *Taxus floridana* could easily be treated as a subspecies of *T. canadensis* (or perhaps of *T. baccata*) on the basis of its morphology, but its ecological tolerances are clearly different. It would be instructive to compare their chemistry in detail to assess the extent of other genetic differences between them.

The genus *Taxus* is most similar to the monotypic Chinese *Pseudotaxus*, which differs in having a white rather than a reddish aril, ovuliferous shoots apparently borne directly in the axils of foliage leaves (vs. on dwarf axillary shoots), sterile scales present (vs. absent) between the sporophylls in the microsporangiate strobilus, and epidermal papillae only on the margins of the leaves (vs. on the subsidiary cells of the stomata) (Florin, 1948b). The New

Caledonian *Austrotaxus* is similar to *Taxus* in the general features of its ovular development (Florin, 1948a) and in the presence of taxane alkaloids (Guéritte-Voegelein *et al.*), but it differs substantially in the structure of its microsporangiate strobilus and in having much larger leaves and seeds.

Crossability among species of *Taxus* has not been investigated in a systematic manner, but hybrids between *T. baccata* and *T. cuspidata* (*T.* ×*media* Rehder) and *T. cuspidata* and *T. canadensis* (*T.* ×*Hunnewelliana* Rehder) have originated spontaneously in cultivation (Dallimore & Jackson; Rehder, 1923) and are now commonly planted in the United States.

Taxus is most notable chemically for the apparently ubiquitous presence of taxane alkaloids, an unusual class of diterpene alkaloids (Hegnauer, 1988; Lythgoe; R. W. Miller). Taxol, an alkaloid of this group that was isolated first from *T. brevifolia* and later from *T. baccata, T. cuspidata,* and *T. Wallichiana* Zucc., has been of particular interest as an antimitotic agent with activity against a number of types of cancer cells (Guéritte-Voegelein *et al.*; Kingston *et al.*; Wani *et al.*). Taxol and related compounds bind to tubulin and promote unusually rapid microtubule assembly and are thus also useful in studying the mitotic process (Bajer *et al.*; Schiff *et al.*). The well-known toxicity of virtually all parts of the yew plant (only the aril is edible) is due in large part to more immediate physiological effects of the various taxane alkaloids, although other biologically active compounds are also present. The degree of toxicity of the foliage appears to vary considerably within species.

Cyanogenic glycosides have been found in the leaves of *Taxus baccata, T. canadensis,* and *T. cuspidata* (Hegnauer, 1986) and presumably contribute to the toxicity of the plants. Biflavonoids and other types of glycosides may also have important pharmacological effects and are probably the active ingredients in nonalkaloidal leaf extracts used in traditional medicine in India (M. S. Y. Khan *et al.*; Vohora).

The ecdysterones, biologically active compounds related to insect-molting hormones, are another interesting class of compounds found in the foliage of at least *Taxus baccata* and *T. cuspidata* (Hegnauer, 1986).

Yews (*Taxus baccata*) have long been important plants in the history and folklore of Great Britain and Europe (Bean; Bialobok; Voliotis). The wood of *Taxus* is very strong and durable and was heavily utilized for the manufacture of bows for archery before the advent of gunpowder. The early Celts, who considered yew trees to be sacred, built temples near them in Britain and Ireland. These temples were often perpetuated by later Christian churches (Bean). Today the main economic importance of *Taxus* is as an ornamental hedge, shrub, or tree. The most widely used horticultural yews are forms of *T. baccata, T. cuspidata* (which is more cold tolerant), and their hybrid, *T.* ×*media.*

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GENERIC LIMITS AND TAXONOMY OF BRAYOPSIS AND EUDEMA (BRASSICACEAE)

IHSAN A. AL-SHEHBAZ[1]

Brayopsis colombiana subsp. *colombiana, B. colombiana* subsp. *ecuadoriana,* and *Eudema incurva* are described as new. They represent first generic records from Colombia, Ecuador, and Peru, respectively. A new combination, *Eudema nubigena* subsp. *remyana,* is proposed. The limits of *Brayopsis* and *Eudema* are critically evaluated, and keys to the species of both genera are given. The sectional classification of *Eudema* is discussed, and its value is questioned.

In his treatment of the Brassicaceae (Cruciferae) for the *Flora of Peru,* Macbride (1938) followed Baehni and Macbride (1937) in uniting *Brayopsis* Gilg & Muschler with the earlier-published *Englerocharis* Muschler. Evidence supporting the maintenance of both genera was given in Al-Shehbaz (1989a); there I pointed out that *Brayopsis* and *Englerocharis* are unrelated to each other, and that their nearest relatives are *Eudema* Humb. & Bonpl. and *Catadysia* O. E. Schulz, respectively.

During the study of some Colombian species of *Draba* L. (Al-Shehbaz, 1989b), I discovered an undescribed species of *Brayopsis* among undetermined material. The new species, hereafter *Brayopsis colombiana* Al-Shehbaz, raised some taxonomic and phytogeographic questions. First, the genus had not previously been reported from Colombia; second, *B. colombiana* is disjunct from the nearest range of *Brayopsis* in Peru by at least 1600 air kilometers; and third, one of the close relatives of this plant is a Bolivian species that Schulz (1924) treated as *Eudema diapensioides* (Wedd.) O. E. Schulz (= *B. diapensioides* (Wedd.) Gilg & Muschler). The phytogeographic disjunctions of *Brayopsis* are not surprising, and several other South American genera of the Brassicaceae show even more dramatic distributional gaps; these will be dealt with in a forthcoming paper. Adequate material of this complex was not available to me 18 months ago when I submitted a revision of *Brayopsis* for publication (Al-Shehbaz, 1989a). The subsequent discovery of *B. colombiana* and *E. incurva* and the study of almost all the types of *Eudema* have prompted a critical reevaluation of the boundaries between these two genera.

Brayopsis resembles *Eudema* in habit and in having few to several solitary flowers borne on peduncles that arise from the center of a well-developed rosette. The maturation of these flowers follows a racemose, centripetal pattern; the direction of anthesis is from the periphery to the center. No other South

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Journal of the Arnold Arboretum **71:** 93–109. January, 1990.

American genera have such a synapomorphy, and therefore *Brayopsis* and *Eudema* are sister groups. The somewhat remotely related *Dactylocardamum* Al-Shehbaz and *Xerodraba* Skottsb. have only one pedunculate or subsessile flower from the center of the leaf cluster terminating a given branch (Al-Shehbaz, 1989c).

Schulz (1924, 1936) separated *Brayopsis* from *Eudema* solely on the basis of its having siliquose instead of siliculose fruits. Additional morphological differences between the two genera, particularly in funicle length and seed-coat sculpture, are also found (see TABLE, FIGURE 1). These differences strongly support the maintenance of both genera.

Brayopsis colombiana is a perfectly good representative of the genus, and characters of the fruits, as well as the filiform funicles and the seed sculpture (see FIGURES 1, 2; TABLE), strongly define its generic identity. Schulz's (1924) initial assignment of *B. diapensioides* to *Eudema* was based solely on his study of a fragmentary isotype at Berlin. Although I have seen only three additional specimens of the type collection, the fruit shape and dimensions, funicle type, and seed-coat sculpture are characteristic of *Brayopsis* and not *Eudema* (see TABLE). Therefore, I believe that Gilg & Muschler's (1909) placement of *B. diapensioides* in *Brayopsis* is more acceptable than its assignment by Schulz (1924) to *Eudema*.

BRAYOPSIS

The taxonomy of *Brayopsis alpaminae* Gilg & Muschler, *B. calycina* (Desv.) Gilg & Muschler, and *B. monimocalyx* O. E. Schulz has been studied in some detail (Al-Shehbaz, 1989a), and therefore an account need not be repeated here. The addition of *B. diapensioides* has expanded the morphological diversity within the genus only a little. A key to the five species of *Brayopsis* and a taxonomic account of *B. colombiana* and *B. diapensioides* are given below.

A. Styles in fruit 1–3 mm long; sepals erect, somewhat coherent; fruit valves densely covered with long, straight trichomes. ..... *B. alpaminae.*

A. Styles in fruit obsolete or 0.2–0.8(–1) mm long; sepals ascending, free; fruit valves glabrous or rarely with short, crisped trichomes.

B. Leaves 0.4–0.8(–1) mm wide, ciliate with trichomes 0.2–0.3 mm long; fruits stipitate; gynophores 1.2–2.5 mm long, thinner than fruiting peduncle. ..... *B. diapensioides.*

B. Leaves 1.5–4 mm wide, glabrous or ciliate with trichomes (0.8–)1–1.5 mm long; fruits sessile, or if stipitate, then gynophores up to 0.5 mm long and thicker than fruiting peduncle.

C. Sepals persistent even after fruit dehiscence; leaves ovate, densely pubescent on upper surface. ..... *B. monimocalyx.*

C. Sepals usually caducous shortly after anthesis; leaves oblong, lanceolate, or linear, glabrous or pubescent on upper surface.

D. Fruits short-stipitate; fruiting peduncles 3–15 mm long; leaves spatulate to oblanceolate or rarely lanceolate; styles conspicuous, to 1.5 mm long; Colombia and Ecuador. ..... *B. colombiana.*

D. Fruits sessile; fruiting peduncles (9–)12–42(–55) mm long; leaves linear to lanceolate; styles obsolete or very rarely to 0.8 mm long; Argentina, Bolivia, Peru. ..... *B. calycina.*

Comparison between Brayopsis and Eudema.

Character	Taxon			
	Brayopsis	*B. colombiana*	*B. diapensioides*	*Eudema*
Fruits				
Shape	Linear, lanceolate, or oblong-linear	Lanceolate	Lanceolate	Oblong, ovoid, suborbicular, obovoid, or pyriform
Length/width quotient	(3.5–)5–8(–10)	5–6.5	3.5–5	1–1.5(–2.5)
Funicle	Long, filiform	Long, filiform	Long, filiform	Short, thick
Septum	Complete	Complete	Complete?	Complete or reduced to rim
Seed-coat sculpture	Colliculate-reticulate	Colliculate-reticulate	Colliculate-reticulate	Coarsely reticulate*

*Mature seeds of only *E. incurva, E. nubigena,* and *E. rupestris* were available.

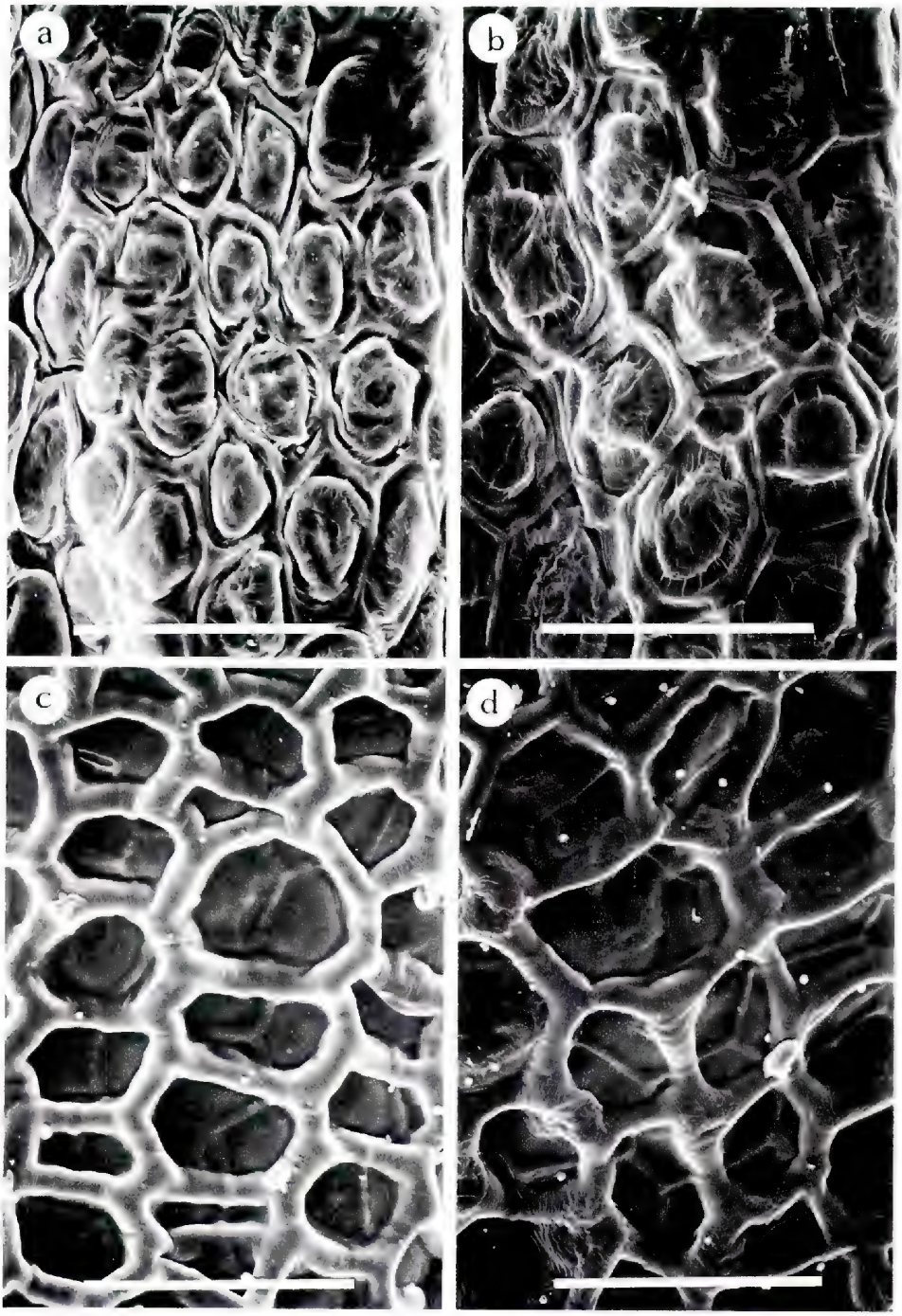

FIGURE 1. Scanning electron micrographs of seeds of *Brayopsis* and *Eudema*: a, *B. alpaminae* (*Macbride & Featherstone 887*, GH); b, *B. colombiana* subsp. *colombiana* (holotype, GH); c, *E. nubigena* subsp. *nubigena* (*Mexia 7652*, F); d, *E. rupestris* (*Jameson s.n.*, US). Scale bars = 100 μm.

Brayopsis colombiana Al-Shehbaz, sp. nov. FIGURE 2.

Herba perenna dense caespitosa, caudicibus ramosis, foliis emortuis persistentibus vestitis. Folia rosulata, spathulata vel oblanceolata, ciliata, 4–12 mm longa, 1.5–4 mm lata, pilis simplicibus (0.8–)1–1.5 mm longis. Pedunculi fructiferi tenui, 3–15 mm longi. Petala alba, spathulata 2.2–2.5 mm longa, 0.7–0.9 mm lata. Siliqua lanceolata, subtereta, breve stipitata, 6–8 mm longa, 1.2–1.5 mm lata; septum hyalinum completum; locula 4–6 sperma; stylus 0.4–1 mm longus. Semina oblonga notorrhiza, brunnea, 1.4–1.6 mm longa, 0.7–0.9 mm lata; funiculi filiformi, 1.2–2 mm longi.

Cespitose, cushion-forming perennials; caudices woody, branched, covered with whole leaves of previous years. Leaves forming dense rosettes, spatulate to oblanceolate, 4–12 mm long, 1.5–4 mm wide, obtuse to subacute at apex, ciliate with trichomes (0.8–)1–1.5 mm long, cuneate at base. Sepals erect, ovate, ca. 2 mm long. Petals white, spatulate, 2.2–2.5 mm long, 0.7–0.9 mm wide. Filaments 1.2–1.8 mm long; anthers ovate, ca. 0.6 mm long. Fruiting peduncles erect, slender, 3–15 mm long, sparsely pubescent. Fruits lanceolate, 6–8 mm long, 1.2–1.5 mm wide, dehiscent, subterete, exserted well above leaf rosette; gynophores stout, to 0.5 mm long; valves glabrous, acute at both ends, inconspicuously veined; septa hyaline, complete; styles 0.4–1 mm long. Seeds 4 to 6 per locule, oblong, 1.4–1.6 mm long, 0.7–0.9 mm wide, brown, pendulous; cotyledons incumbent; funicles filiform, 1.2–2 mm long.

TYPE. Colombia, Depto. Boyacá, Cordillera Oriental, Sierra Nevada del Cocuy, Alto Ritacuva, 11 April 1959, 4600 m alt., *H. G. Barclay & P. Juajibioy 7355* (holotype, GH; isotype, MO).

KEY TO THE SUBSPECIES

Leaves ciliate; sepals ca. 2 mm long; petals 2.2–2.5 mm long; styles in fruit 0.4–1 mm long; Colombia. ..... 2a. subsp. *colombiana.*
Leaves not ciliate; sepals 3–4.5 mm long; petals 4–5.5 mm long; styles in fruit 1–1.5 mm long; Ecuador. ..... 2b. subsp. *ecuadoriana.*

2a. **Brayopsis colombiana** subsp. **colombiana**

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** DEPTO. BOYACÁ: Cordillera Oriental, Sierra Nevada del Cocuy, Alto Ritacuva, 4400 m alt., *Barclay & Juajibioy 7410* (GH); same locality, 4600 m alt., *Grubb, Curry, & Fernández-Pérez 304* (K, US).

Brayopsis colombiana subsp. *colombiana* is the sole representative of the genus in Colombia. It grows on unstabilized, fine, sandy soil in crevices of bedrock above moraines of the Ritacuva glacier at an altitude of ca. 4400–4600 m.

2b. **Brayopsis colombiana** subsp. **ecuadoriana** Al-Shehbaz, subsp. nov.

Folia glabra, nonciliata; sepala 3–4.5 mm longa; petala 4–5.5 mm longa, ca. 1.5 mm lata; stylus 1–1.5 mm longus.

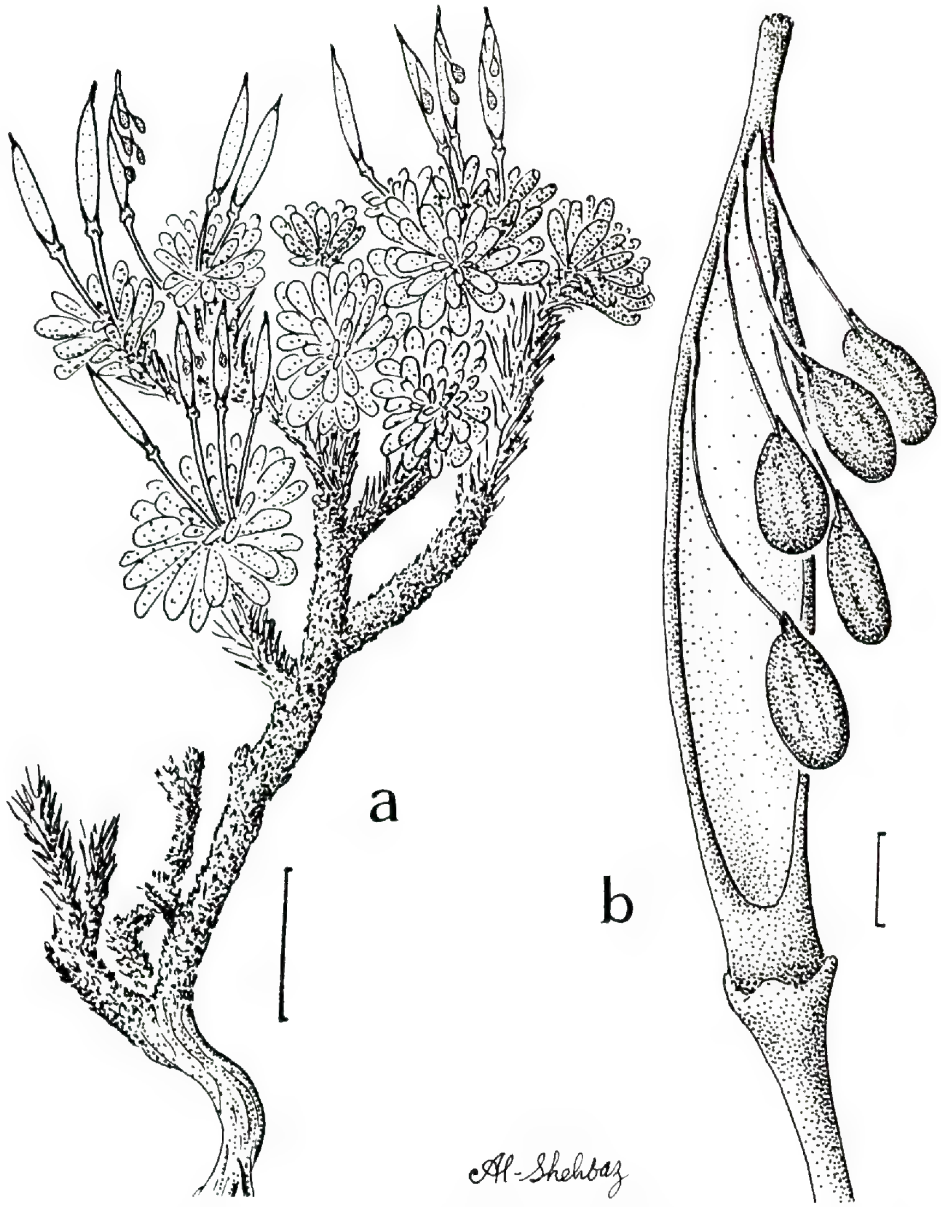

FIGURE 2. *Brayopsis colombiana* subsp. *colombiana* (holotype): a, plant; b, fruit with valves removed. Scale bars = 1 cm (a), 1 mm (b).

Leaves glabrous, lanceolate to oblanceolate, not ciliate. Sepals oblong, 3–4.5 mm long. Petals white, spatulate, 4–5.5 mm long, ca. 1.5 mm wide. Fruits 5–6 mm long; styles 1–1.5 mm long.

TYPE. Ecuador, Prov. Azuay, páramo de las Cajas, Lagunas Suerococha, 35 km on Cuenca-Molleturo road; mountain 1 km NW of pass, 79°14′W, 2°48′S, 4200–4400 m alt., 30 Jan. 1988, *U. Molau & B. Eriksen 2787* (holotype, GB).

The type collection of *Brayopsis colombiana* subsp. *ecuadoriana* represents

the first record of *Brayopsis* from Ecuador, and the type locality somewhat bridges the gap between the main range of the genus and that of subsp. *colombiana*. The differences in flower size between the two subspecies is significant. In the absence of additional material, and because of the evident similarity in all other morphological characters, I have refrained from recognizing these taxa as separate species. The presence vs. absence of leaf trichomes, which is a good distinguishing character, should not be overemphasized: the same pattern occurs within *B. calycina*.

Brayopsis colombiana resembles *B. diapensioides* in several features, particularly in having lanceolate, stipitate fruits, short styles, and filiform funicles. It is easily distinguished, however, by its spatulate to oblanceolate or lanceolate leaves 1.5–4 mm wide, its stout gynophores to 0.5 mm long, and its either glabrous or ciliate leaves with fine trichomes (0.8–)1–1.5 mm long. In contrast, *B. diapensioides* has narrowly lanceolate to linear leaves 0.4–0.8(–1) mm wide, slender gynophores 1.2–2.5 mm long, and stouter trichomes 0.2–0.3 mm long. Perhaps the nearest relative of *B. colombiana* is *B. calycina*, from which it is easily distinguished by several characters given in the key above.

Brayopsis diapensioides (Wedd.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 484. 1909.

Draba diapensioides Wedd. Ann. Sci. Nat. Bot. **5**(1): 285. 1864. *Eudema diapensioides* (Wedd.) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 245. 1924. TYPE: Bolivia, Prov. Larecaja, vicinity of Sorata, between Ancouma and Turelague in Cerro de Aosas, 4500 m alt., November 1860, *Mandon 894* (holotype, P!; isotypes, B! (photos, F!, GH!), BM!, G!).

Densely cespitose perennials, with thick, much-branched caudices covered with persistent petiolar remains of previous years. Leaves narrowly lanceolate to linear, forming well-developed rosettes, 4–8 mm long, 0.4–0.8(–1) mm wide, subacute, ciliate with unbranched trichomes 0.2–0.3 mm long; blades thin, shorter than persistent, conspicuously thickened petioles. Sepals erect, ovate, 2–2.5 mm long, 1.2–1.3 mm wide, membranaceous at margin, glabrous. Petals obovate, 2.5–3.5 mm long, 1.2–1.5 mm wide, cuneate at base. Filaments 2–2.5 mm long; anthers ovate, 0.5–0.6 mm long. Fruiting peduncles 5–8 mm long, thick, up to 1 mm wide, sparsely pubescent with trichomes to 0.3 mm long. Fruits lanceolate, subterete, 3.5–5 mm long (excluding style and gynophore), stipitate, glabrous; styles 0.4–0.7 mm long; gynophores 1.2–2.5 mm long, slender, about half as wide as fruiting peduncle. Seeds oblong, 1.2–1.4 mm long, 0.7–0.8 mm wide, borne on filiform funicles ca. 1.2 mm long.

Hardly anything can be said about the variation and biology of this species, which is apparently known only from the type collection. *Brayopsis diapensioides* can easily be distinguished from the remainder of the genus in having slender gynophores much narrower than the thickened fruiting pedicels.

EUDEMA

As interpreted here, *Eudema* consists of six species, including only five of the eight recognized by Schulz (1924, 1936). One species, *E. remyana* (Wedd.)

O. E. Schulz, is reduced here to a subspecies of *E. nubigena* Humb. & Bonpl. Another, *E. diapensioides,* is treated above as a species of *Brayopsis.* The third species, *E. colobanthoides* (Skottsb.) O. E. Schulz, is reassigned to *Xerodraba.* The sixth species, *E. incurva,* is described below as new.

Schulz (1924, 1936) recognized the heterogeneity of *Eudema* and divided the genus into four sections. The monotypic sect. *Gynophoridium* O. E. Schulz was defined solely on the basis of having stipitate instead of sessile fruit. Its single species is recognized here as *Brayopsis diapensioides.*

Section *Lepteudema* O. E. Schulz is separated from the rest of the genus mainly on the basis of having slender, scaly, loosely branched rhizomes instead of a thick caudex. Two species of this section, *Eudema friesii* O. E. Schulz and *E. werdermannii* O. E. Schulz, have dendritic leaf trichomes that are lacking in the rest of the genus. This section might justifiably be raised to a separate genus, but in the absence of adequate material at my disposal, I refrain from taking such an action.

The monotypic sect. *Xereudema* O. E. Schulz is based on a species that was originally described as *Xerodraba colobanthoides* Skottsb. Schulz (1924) transferred the species to *Eudema* because it allegedly lacks the expanded leaf bases, subsaccate sepals, and somewhat fleshy petals characteristic of *Xerodraba.* However, these features are unreliable in this complex, and *Xerodraba* is easily separated from *Eudema* by its solitary terminal flowers, usually complete septum, and densely imbricate, minute, fleshy, wholly persistent leaves. *Eudema* has several flowers at the branch apex, a usually rudimentary septum, and nonimbricate, large, unfleshy leaves with persistent petioles.

Boelcke (1982) transferred *Xerodraba colobanthoides* to the later homonym *Skottsbergiella* Boelcke and then (in Boelcke & Romanczuk, 1984) to *Skottsbergianthus* Boelcke. However, the single character on which the latter genus is based, the presence of a minute, scalelike appendage at the base of each petal, might not justify its recognition as distinct from *Xerodraba.* I have not seen adequate material of *X. colobanthoides,* but the species does not belong to *Eudema.* I have concluded that Schulz's (1924, 1936) sectional classification of *Eudema* is artificial and does not improve the taxonomy of the genus.

Eudema Humb. & Bonpl. Pl. Aequinoct. **2:** 133. 1813. LECTOTYPE (here designated): *E. rupestris* Humb. & Bonpl.

Cespitose, scapose perennials with thick, branched caudices or slender rhizomes, the branches covered with petiolar remains of previous years and terminated by rosettes; trichomes simple or dendritic, sometimes absent. Leaves rosulate, petiolate, somewhat fleshy, entire or rarely pinnately lobed; petioles persistent, thick or flattened at base. Flowers solitary, borne on peduncles originating from center of rosette, maturing centripetally. Sepals erect, ovate, nonsaccate at base, caducous. Petals white to creamy white, obovate, spatulate, oblanceolate, or sublinear, usually not differentiated into blade and claw. Stamens 6; anthers oblong to ovate. Nectar glands 4, 1 on each side of a lateral stamen. Fruits dehiscent, suborbicular, ovoid, obovoid, pyriform, or rarely oblong, subterete to conspicuously flattened parallel or rarely perpendicular to

replum, glabrous; septa reduced to narrow rim or rarely complete; stigmas subentire. Seeds few to many, coarsely reticulate; cotyledons incumbent; funicles short, thick.

Key to the Species of Eudema

A. Leaves with dendritic trichomes; plants with slender rhizomes.
  B. Leaves pinnately lobed, rarely coarsely toothed, upper surface sparsely pubescent. ..... 6. *E. friesii.*
  B. Leaves entire, upper surface densely pubescent. ..... 5. *E. werdermannii.*
A. Leaves glabrous or with simple trichomes; plants with thick caudices (if with rhizomes, then leaves glabrous and fruits flattened).
  C. Fruits obovate to pyriform, conspicuously flattened parallel to replum; plants rhizomatous. ..... 4. *E. hauthalii.*
  C. Fruits oblong or ovoid, subterete or slightly flattened; plants with thick caudex.
    D. Fruits oblong; seeds 10 to 30 on each placenta; petioles flattened at base; leaves linear to narrowly oblanceolate, glabrous.
      E. Leaf blades ciliate; septa complete; fruits strongly incurved; seeds plump, 15 to 30 on each placenta, 0.7–0.8 mm long. ..... 1. *E. incurva.*
      E. Leaf blades not ciliate; septa reduced to rim; fruits straight; seeds flattened, 10 to 13 on each placenta, 1.2–1.7 mm long. ..... 2. *E. rupestris.*
    D. Fruits ovoid; seeds 1 to 5 on each placenta; petioles thick at base; leaves spatulate to ovate or oblanceolate, ciliate or glabrous. ..... 3. *E. nubigena.*

1. **Eudema incurva** Al-Shehbaz, sp. nov. FIGURE 3.

Herba perenna caespitosa scaposa, caudicibus tenuibus. Folia rosulata lineari vel lineari-lanceolata, ciliata, 5–15 mm longa, 0.6–1.4 mm lata, petiolis persistentibus, ad basin complanatibus. Pedunculi fructiferi glabri, 4–10 mm longi. Siliqua oblonga, incurva, angustiseptata, 4–8 mm longa, 2.5–3.5 mm lata; septum hyalinum completum; locula 15–30-sperma; stylus 0.4–0.7 mm longus. Semina late ovoidea, notorrhiza, biseriata, reticulata, 0.7–0.8 mm longa, 0.5–0.6 mm lata.

Cespitose, perennial herbs with slender, simple, or few-branched caudices covered with petiolar remains of previous years. Leaves rosulate, petiolate, linear to linear-lanceolate, 5–15 mm long, 0.6–1.4 mm wide, ciliate with unbranched, straight trichomes to 2 mm long; petioles persistent, not ciliate, flattened at base, 2–7 mm long. Flowers not seen. Fruiting peduncles glabrous, 4–10 mm long. Fruits oblong, strongly incurved, glabrous, 4–8 mm long, 2.5–3.5 mm wide, flattened contrary to septum, rounded at apex and base; septa complete, hyaline; styles 0.4–0.7 mm long. Seeds 15 to 30 per locule, broadly ovoid, plump, 0.7–0.8 mm long, 0.5–0.6 mm wide, dark brown, conspicuously reticulate, biseriately arranged in each locule; funicles 0.2–0.5 mm long; cotyledons incumbent.

TYPE. Peru, Depto. Ancash, Prov. Huaraz, Punta Callán and above, summit area of the Huaraz-Casma road, 30 km from Huaraz, 1–3 km N of road, heavily grazed puna with rock outcrops, 77°37′W, 9°32′S, 4200–4400 m alt., 7 April 1988, *U. Molau & B. Eriksen 3512* (holotype, GB (photocopy, GH)).

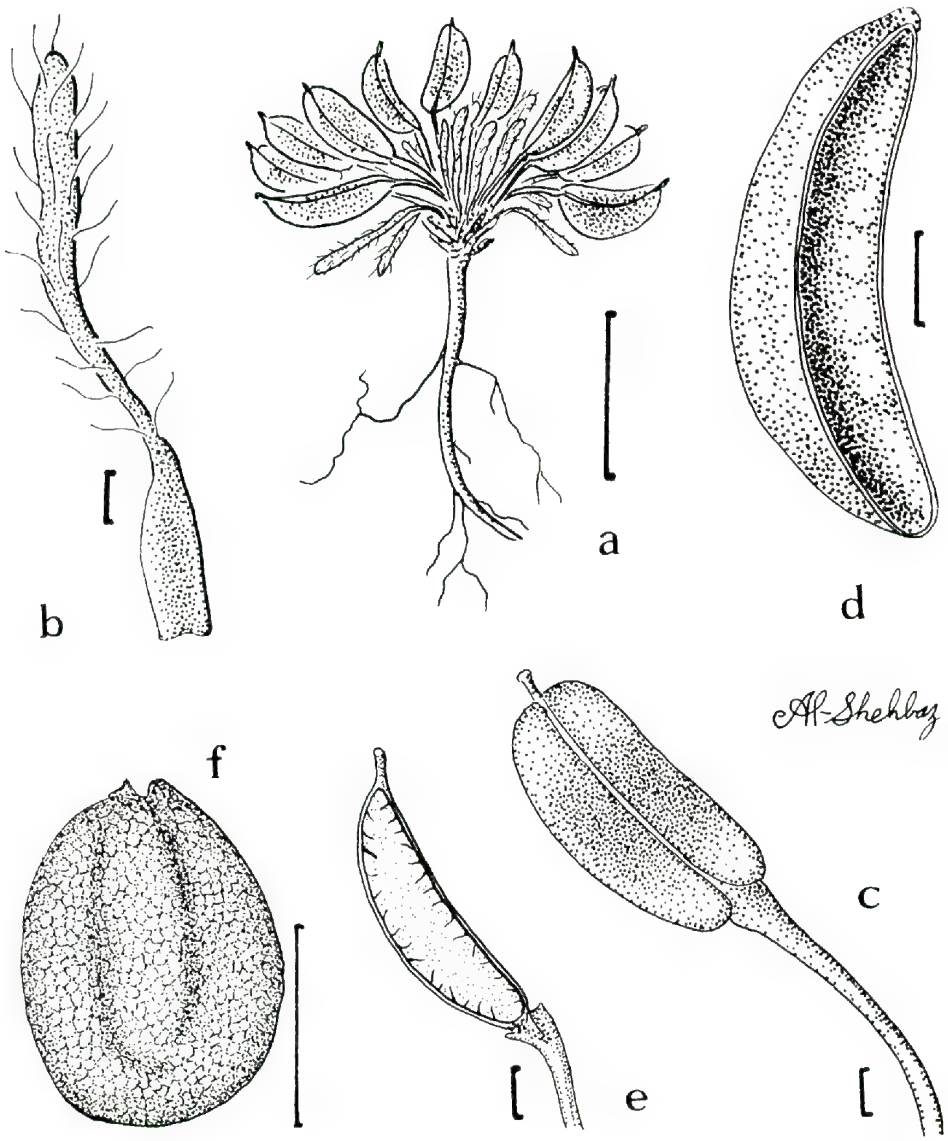

FIGURE 3. *Eudema incurva* (holotype): a, plant; b, leaf; c, fruit; d, valve; e, replum and septum; f, seed. Scale bars = 1 cm (a), 1 mm (b–f).

Eudema incurva is closely related to the Ecuadorian endemic *E. rupestris*. It is easily distinguished from the remainder of the genus in having angustiseptate, strongly incurved fruits, a complete septum, many (15 to 30 per locule) biseriately arranged, small seeds to 0.8 mm long, and conspicuously ciliate leaf blades with trichomes to 2 mm long. No flowers are found on any of the six plants of the holotype. However, floral remains on a young fruit reveal that the sepals are oblong, pubescent, and ca. 2.5 mm long, and that the filaments and the oblong anthers are ca. 2 and 0.8 mm long, respectively.

Eudema incurva is somewhat anomalous in the genus because it has a com-

plete instead of a rimlike septum and numerous seeds per locule. In these characters it resembles *Brayopsis,* but the overall morphology strongly supports its placement in *Eudema.*

2. **Eudema rupestris** Humb. & Bonpl. Pl. Aequinoct. **2:** 133. 1813.

Sisymbrium rupestre (Humb. & Bonpl.) Wedd. Ann. Sci. Nat. Bot. **5**(1): 290. 1864; *Hesperis rupestris* (Humb. & Bonpl.) Kuntze, Revis. Gen. Pl. **2:** 935. 1891; *Draba humboldtii* Desv. J. Bot. (Desvaux) **3:** 171. 1815; *Eutrema humboldtii* (Desv.) Sprengel, Syst. Veg. **2:** 880. 1825. TYPE: Ecuador, between Quito and Cuenca, Montaña del Assuay, *Humboldt & Bonpland s.n.* (holotype, P (IDC 6209. 119: I. 6!); isotype, B!).

Eudema grandiflora Planchon *in* W. J. Hooker, London J. Bot. **3:** 620. 1844; *Sisymbrium grandiflorum* (Planchon) Wedd. Ann. Sci. Nat. Bot. **5**(1): 290. 1864; *Hesperis planchoniana* Kuntze, Revis. Gen. Pl. **2:** 936. 1891; *Brayopsis grandiflora* (Planchon) Gilg & Muschler, Bot. Jahrb. Syst. **42:** 482. 1909. TYPE: Ecuador, Andes, monte Assuay, 15,000 ft [ca. 4570 m] alt., *Jameson s.n.* (holotype, MPU or NA; isotype, NY!).

Cespitose, glabrous perennials with much-branched caudices covered with petiolar remains of previous years. Leaves numerous, rosulate, petiolate; blades linear to narrowly oblanceolate, rounded at apex, entire, attenuate at base, 7–17 mm long, 1–3 mm wide; petioles conspicuously flattened at base, 7–10 mm long. Sepals erect, narrowly oblong to sublanceolate, 6–7 mm long, ca. 2 mm wide, scarious at margin, with few subapical trichomes. Petals oblong to sublinear, 11–12 mm long, ca. 2 mm wide. Filaments erect, slender, 5.5–6.5 mm long; anthers narrowly oblong, 1.2–1.5 mm long. Fruiting peduncles glabrous, 10–14 mm long. Fruits oblong, subterete to slightly compressed contrary to replum; valves thin, glabrous, with conspicuous midvein; septa reduced to rim; styles slender, 3–3.5 mm long. Seeds about 10 to 13 on each placenta, ovoid, slightly compressed, 1.2–1.7 mm long, 0.8–1.1 mm wide, dark brown to blackish, conspicuously reticulate; funicles thick, ca. 0.2–0.5 mm long.

REPRESENTATIVE SPECIMENS. **Ecuador:** Andes above Quito, 14,000 ft [ca. 4267 m] alt., *Jameson s.n.* (US, 2 sheets).

Eudema rupestris is apparently a very rare species. I have examined only a few specimens, which were collected around the middle of the last century. It is easily distinguished from its nearest relative, *E. nubigena,* in having oblong fruits with 10 to 13 seeds on each placenta, larger flowers with longer sepals, petals, and anthers, and linear to narrowly oblanceolate leaves with flattened petioles. In *E. nubigena* the ovoid fruits have 1 to 5 seeds on each placenta, the flowers are smaller, and the leaves are usually spatulate to ovate with thick petioles.

3. **Eudema nubigena** Humb. & Bonpl. Pl. Aequinoct. **2:** 136. 1813.

Densely cespitose perennials forming well-developed cushions. Caudices woody, much branched, densely covered with persistent petioles of previous years. Leaves numerous, forming dense rosettes, somewhat fleshy; blades spatulate to oblanceolate or ovate, (3–)4–8(–9) mm long, 1.5–4(–5) mm wide, entire,

obtuse to somewhat subacute, nonciliate or ciliate throughout, with unbranched trichomes to 1.2 mm long; petioles persistent, thick, (2–)3–10 mm long. Sepals ovate to oblong, (2–)2.5–3.5(–6) mm long, (1.2–)1.5–2 mm wide, scarious at margin. Petals broadly obovate, 3–5 mm long, 1.5–2.5(–2.8) mm wide, rounded at apex, not clawed, white to creamy white. Filaments 2–3(–3.5) mm long; anthers oblong, 0.7–1 mm long, usually violet. Fruiting peduncles 2–5(–10) mm long. Fruits broadly to narrowly ovoid, subterete, (2–)3–5(–6) mm long, 2–3 mm wide; septa usually reduced to narrow rim; styles 0.4–2.5(–3) mm long. Seeds (1 or) 2 to 4 (or 5) on each placenta, oblong-ovate, (1.4–)1.6–2 mm long, (0.8–)1–1.3(–1.4) mm wide; dark brown, conspicuously reticulate; funicles thick, to 0.6 mm long.

KEY TO THE SUBSPECIES

Leaf blades conspicuously ciliate; fruits usually broadly ovoid, styles 0.4–1.5(–3) long. ..... 3a. subsp. *nubigena.*

Leaf blades usually not ciliate; fruits narrowly to broadly ovoid, styles (1.2–)1.5–2.5(–3) mm long. ..... 3b. subsp. *remyana.*

3a. **Eudema nubigena** subsp. **nubigena**

Draba nubigena (Humb. & Bonpl.) Desv. J. Bot. (Desvaux) **3:** 171. 1815; *Sisymbrium nubigenum* (Humb. & Bonpl.) Wedd. Ann. Sci. Nat. Bot. **5**(1): 290. 1864; *Hesperis nubigena* (Humb. & Bonpl.) Kuntze, Revis. Gen. Pl. **2:** 935. 1891; *Eutrema bonplandii* Sprengel, Syst. Veg. **2:** 880. 1825. TYPE: Ecuador, between Quito and Cuenca, Montaña del Assuay, *Humboldt & Bonpland s.n.* (holotype, P (IDC 6209. 119: I. 7!)).

Leaf blades ciliate throughout, with trichomes to 1.2 mm long. Fruits broadly or rarely narrowly ovoid, usually plump; styles stout to rarely slender, 0.4–1.5(–3) mm long.

REPRESENTATIVE SPECIMENS. **Ecuador.** PROV. IMBABURA: volcano Cotacachi, *Boysen Larsen, Eriksen, Kvist, Nissen, & Korning 45635* (AAU); Imbabura, *Hirsch 155* (GH); Cayambe Mt., *Cazalet & Pennington 5735* (UC). PROV. PICHINCHA: Cerro Antisana, *Grubb, Lloyd, Pennington, & Whitmore 632* (NY); Pichincha and Antisana, *Sodiro 52* (B); Loma Pilongo, NE slope of Nevado Iliniza, *Molau & Eriksen 2269* (GB); Cerro Iliniza, near border to Cotopaxi, *Harling 11175* (GB); W Rucu Pinchincha, Padre Encantado, *Molau, Eriksen, & Klitgaard 2407, 2408* (GB); Mt. Corazón, *Asplund 17499* (G, NY, S); Volcán Iliniza, *Sparre 17457* (S); summit of Cerro Pichincha, *Holmgren & Heilborn 175* (S, 2 sheets); Mt. Pichincha, near Quito, *Hitchcock 21064* (GH, NY, US); Rucu Pichincha, *Asplund 17310* (NY, S); Volcán de Pichincha, *Bell 362* (BM, 2 sheets), *Mexia 7652* (F, UC, US); Andes above Quito, *Jameson 11* (LE), *33* (G, GH, P), *752* (BM, G, LE); on Chimborazo and Pichincha, *Jameson s.n.*, Sept. 1824 (E).

Subspecies *nubigena* grows on consolidated moraine and sandy soil between rocks or in crevices, as well as in grass paramo at altitudes of 4000–4820 m.

Plants of this subspecies vary in flower color from white (*Boysen Larsen et al. 45635*) to greenish yellow (*Grubb et al. 632*). Style length is also variable: styles of most plants that I have examined are usually less than 1.5 mm long, while those of plants comprising *Sparre 17457* are up to 3 mm. Although the

septum in almost all collections of subsp. *nubigena* is reduced to a narrow rim, it is unusually complete in *Boysen Larsen et al. 45635.*

3b. **Eudema nubigena** subsp. **remyana** (Wedd.) Al-Shehbaz, comb. nov.

Based on *Sisymbrium remyanum* Wedd. Ann. Sci. Nat. Bot. **5**(1): 290. 1864; *Hesperis remyana* (Wedd.) Kuntze, Revis. Gen. Pl. **2**: 935. 1891; *Brayopsis remyana* (Wedd.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 482. 1909; *Eudema remyana* (Wedd.) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 244. 1924. TYPE: Ecuador, Chimborazo, *Remy s.n.,* 3 Nov. 1856 (holotype, P! (photo and fragment, F!)).

Aschersoniodoxa chimborazensis Gilg & Muschler, Bot. Jahrb. Syst. **42**: 470. 1909. TYPE: Ecuador, Chimborazo, *Hall s.n.,* 1853 (holotype, B!).

Leaf blades glabrous throughout, rarely sparsely ciliate. Fruits narrowly ovoid, rarely broadly so; styles slender to rarely stout, (1.2–)1.5–2.5(–3) mm long.

REPRESENTATIVE SPECIMENS. **Ecuador.** PROV. BOLÍVAR: W base of Volcán Chimborazo, *Maguire & Maguire 61738* (NY), *61746* (NY, US); ca. 33 km N of Guaranda, W of Volcán Chimborazo, *Luteyn & Cotton 11076* (GH). PROV. CHIMBORAZO: E slope of Mt. Chimborazo, *Asplund 7934* (S); S slope of Mt. Chimborazo, *Asplund 8384* (CAS, GH, NY, S, US), *8392* (S); WSW slope of Mt. Chimborazo, below Whymper refuge, *Molau & Eriksen 2991* (GB); Chimborazo, *Hirsch E330* (GH), *Whymper s.n.,* Jan. 1880 (BM); slope of Chimborazo, above Tortorillas, *Penland & Summers 702* (GH); between Urbina and Mt. Chimborazo, *Hitchcock 21976* (GH, NY, US); Riobamba, *Primbach 219* (US). PROV. TUNGURAHUA: Las Minas, SE of Volcán Carihuayrazo, *Brandbyge 42383* (AAU); Tungurahua volcano, *Korning & Thomsen 47335* (AAU); paramo of Minza, *Penland & Summers 387* (GH, US).

Subspecies *nubigena* and *remyana* are remarkably similar in almost all aspects of habit, leaf morphology, floral dimensions, and size and sculpture of seeds, as well as the reduction of the septum to a narrow rim. They are somewhat different in leaf pubescence, style length, fruit shape, and geographic distribution.

Schulz (1924) separated the two subspecies (as species) solely on the basis of the leaves being ciliate in subsp. *nubigena* and nonciliate in subsp. *remyana.* This difference holds for the majority of collections that belong to the latter taxon. However, in *Luteyn & Cotton 11076* leaf blades and/or petioles vary continuously from completely glabrous to sparsely pubescent. Ciliate and nonciliate petioles have also been observed in *Asplund 8384* (NY).

The fruits of subsp. *nubigena* are usually broadly ovoid, while those of subsp. *remyana* tend to be narrower. However, some collections of the latter (e.g., *Asplund 8384*; S) have broadly ovate fruits. Styles of subsp. *remyana* are usually longer than those of subsp. *nubigena.* In *Sparre 17457* and *Asplund 17499* (NY), both of subsp. *nubigena,* style length is 2–3 and 1.2–1.8 mm, respectively. Similarly, in a few plants of subsp. *remyana* (e.g., *Asplund 8392*) the styles are 1.2–1.6 mm long.

A critical evaluation of these slight differences in style length, fruit shape, and leaf pubescence reveals that there is no justification for recognizing *Eudema remyana* as a species distinct from the earlier-published *E. nubigena.* The taxonomy of the group is best served by reducing the former to a subordinate taxon of the latter.

Plants of subsp. *remyana* apparently occupy similar habitats at about the same altitude as those of subsp. *nubigena*.

4. **Eudema hauthalii** Gilg & Muschler, Bot. Jahrb. Syst. **42**: 471. 1909.

Brayopsis hauthalii (Gilg & Muschler) Skottsb. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 236. 1916. TYPE: Argentina, [Prov.] Santa Cruz, Río Gallegos, Cerro Buitres, *R. Hauthal 10618* (holotype, B! (photo, F!)).

Brayopsis skottsbergeri Gilg in Skottsberg, Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 236. 1916. TYPE: Patagonia, Sierra de los Baguales, Paso Centinela–Baguales, *Skottsberg s.n.*, 1909 (not seen).

Prostrate, glabrous perennials with slender, branched rhizomes, the branches terminated by rosettes and covered with petiolar remains of previous years. Leaves rosulate, petiolate, oblanceolate-spatulate to narrowly oblanceolate or linear, (6–)9–15(–22) mm long, (0.7–)1–1.5(–2) mm wide, entire, rounded at apex, attenuate at base; petioles glabrous, as long as or longer than blades, conspicuously flattened at base. Sepals erect, ovate, 2.5–3.5 mm long, glabrous, rounded at apex. Petals oblanceolate, (4.5–)5.5–6.5 mm long, (1.2–)1.5–1.8 mm wide, rounded at apex, attenuate at base, creamy white. Filaments slender, 2.5–3.5 mm long; anthers 0.5–0.6 mm long. Fruiting peduncles (3–)5–10 mm long, few to several from center of rosette. Fruits sessile, obovate to pyriform, rarely ovate, flattened parallel to replum, (4–)5–11(–12) mm long, 4–7 mm wide, dehiscing from apex downward; valves thin, glabrous, inconspicuously nerved; septa hyaline, reduced to narrow rim; styles 0.5–1 mm long. Seeds 2 to 5 on each placenta, oblong, 2–2.5(–3) mm long, 1.1–1.3(–1.8) mm wide, light brown, obscurely flattened at distal end; funicles thick.

REPRESENTATIVE SPECIMENS. **Argentina.** PROV. SANTA CRUZ: Depto. Lago Argentino, Ea. Pérez, Río de las Vueltas, Meseta Quemada, *Sleumer 1386* (G, US); Cerro Corona, La Victorina, Lago Paine, *Pisano & Pisano 5603* (GH, HIP); Güer Aike, Ea. Las Viscachas, Ensenada de Riques, *TBPA 2679* (HIP); Co. Sin Nombre, *TBPA 2674* (HIP); Co. Pto. la Piedra, *TBPA 2542* (HIP). **Chile.** MAGALLANES: Depto. Ultima Esperanza, Sierra de los Baguales, Ea. La Cumbre, Co. Sin Nombre, *TBPA 757* (HIP).

Eudema hauthalii is most closely related to *E. werdermannii*, from which it is easily distinguished in having glabrous leaves, obovate to pyriform fruits (4–)5–11(–12) mm long, and seeds 2–2.5(–3) mm long. In contrast, *E. werdermannii* has densely pubescent leaves with dendritic trichomes, suborbicular fruits 2.5–3 mm long, and seeds 0.9–1.2 mm long. The two species resemble each other in habit, leaf morphology, flower size and color, flattening of the fruit, reduction of the septum to a rim, and number of seeds on each placenta.

Eudema hauthalii and *E. werdermannii* form dense cushions in moist seepage areas of rocky steppes. They often produce a tangled growth among fine gravel, particularly at altitudes of 700–1500 m.

5. **Eudema werdermannii** O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem **10**: 462. 1928. TYPE: Chile, Prov. Atacama, Depto. Copiapó, Cord. Río Figueroa, Co. Paredones, ca. 4300 m alt., Jan. 1926, *E. Werdermann 974* (holotype, B! (photos, F!, GH!, NY!); isotypes, F!, GH!, M!, MO!, NY!, S!, UC!, US!, Z!).

Cespitose, rhizomatous perennials forming dense cushions; rhizomes branched, 1–2.5 mm wide, with sessile, ovate to lanceolate scales at nodes. Leaves rosulate, somewhat fleshy, narrowly oblanceolate to spatulate, (3–)8–20(–30) mm long, (0.7–)1–2(–3.5) mm wide, obtuse to rounded at apex, entire, attenuate at base, glabrous on lower surface, usually densely pubescent on upper surface with dendritic trichomes; petioles ciliate with simple or furcate trichomes, somewhat expanded at base. Sepals erect, oblong, 3–4 mm long, 1.4–1.8 mm wide, obtuse at apex, scarious at margin, sparsely pubescent on back with dendritic trichomes. Petals oblanceolate, (4.5–)5–7 mm long, 1.5–2.2 mm wide, rounded at apex, cuneate at base, white to creamy white. Filaments 2.5–3.5 mm long; anthers oblong, 0.8–1 mm long. Fruiting peduncles glabrous, 3.5–20 cm long. Fruits sessile, suborbicular, strongly compressed parallel to replum, 2.5–3 mm in diameter; septa reduced to narrow rim; styles 0.2–0.8 mm long; stigmas capitate, slightly 2-lobed. Seeds 3 to 5 on each placenta, ovoid, 0.9–1.2 mm long, 0.6–0.8 mm wide.

REPRESENTATIVE SPECIMENS. **Argentina:** PROV. SAN JUAN: Quebrada Ortiga, E part of Cordillera de la Ortiga, *Johnston 6174* (BA, GH, S), *6290* (GH); Quebrada de Coucouta, between Las Vicuñitas and el Portezuelo de Coucouta, *Moreau 30/87* (BA); Iglesia, Río Blanco cerca del Baño del Bollete, *Castellanos 15523* (US).

Eudema werdermannii forms prostrate mats in wet gravel at altitudes of 3800 to 4300 m. Field notes on *Johnston 6174* (GH) indicate that the plant produces much-branched rhizomes that form a tangled growth in the gravel, and that the plants are smaller and less branched in drier sites than in wetter areas.

Eudema werdermannii is highly variable in habit and leaf size and shape. Plants of the type collection have much-shortened rhizomes that terminate in a compact, few-branched caudex. In contrast, those of *Johnston 6174* are rather lax and have long, slender rhizomes with a conspicuous, sessile scale at each node. The variation in leaf size and shape is evident within each population, and apparently plants of the drier sites have smaller leaves with shorter petioles than those of the wetter ones.

6. **Eudema friesii** O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 245. 1924. TYPE: Argentina, Prov. Salta, Incachuli bei San Antonio de las Cobras, ca. 5000 m alt., 30 Oct. 1901, *Fries 703* (holotype, B! (photos, F!, GH!, NY!); isotype, UPS!).

Prostrate rhizomatous perennials; rhizomes slender, branched, with conspicuous, sessile scale at each node; branches terminated by rosettes and covered below leaves with petiolar remains of previous years. Leaves rosulate, petiolate, lanceolate to linear, (5–)9–16 mm long, (1.5–)2–3 mm wide, obtuse at apex, pinnately lobed to rarely dentate at margin, glabrous on lower surface, sparsely pubescent on upper surface and margin with dendritic trichomes. Flowering peduncles originating from center of rosette, 2–4 mm long. Sepals erect, ovate, 2.5–3.5 mm long, ca. 1.5 mm wide, glabrous or sparsely pubescent below apex, scarious at margin. Petals spatulate, 5–6.5 mm long, 1.2–1.5 mm wide, creamy white, rounded at apex, attenuate to clawlike base. Filaments 3–3.5 mm long; anthers oblong, 0.9–1 mm long. Young fruits ovate, apparently

compressed parallel to replum, glabrous; septa reduced to narrow rim; styles ca. 0.5 mm long. Seeds not seen.

ADDITIONAL SPECIMEN EXAMINED. **Bolivia.** DEPTO. ORURO: Prov. Carangas, Sajama, 4200 m alt., *Asplund 3988* (S).

Eudema friesii is a very rare species that apparently grows on fine gravel. Its nearest relative is *E. werdermannii,* which it resembles in having branched trichomes, slender rhizomes, and creamy white flowers. It is easily distinguished from the remaining species of *Eudema* by its pinnately lobed instead of entire leaves.

EXCLUDED NAMES

Eudema colobanthoides (Skottsb.) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 246. 1924. = **Xerodraba colobanthoides** Skottsb. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 234. 1916.

Eudema diapensioides (Wedd.) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 245. 1924. = **Brayopsis diapensioides** (Wedd.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 484. 1909.

Eudema glebaria (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 472. 1909. = **Xerodraba glebaria** (Speg.) Skottsb. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.

Eudema lycopodioides (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 471. 1909. = **Xerodraba lycopodioides** (Speg.) Skottsb. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.

Eudema microphylla (Gilg) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 472. 1909. = **Xerodraba pycnophylloides** (Speg.) Skottsb. var. **microphylla** (Gilg) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 250. 1924.

Eudema monantha (Gilg) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 472. 1909. = **Xerodraba monantha** (Gilg) Skottsb. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.

Eudema patagonica (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 471. 1909. = **Xerodraba patagonica** (Speg.) Skottsb. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.

Eudema pectinata (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 471. 1909. = **Xerodraba pectinata** (Speg.) Skottsb. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 235. 1916.

Eudema pycnophylloides (Speg.) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 471. 1909. = **Xerodraba pycnophylloides** (Speg.) Skottsb. Kongl. Svenska Vetenskapsakad. Handl. **56**(5): 362. 1916.

Eudema thlaspiforme Philippi, Anales Univ. Chile **41**: 675. 1872. = **Draba philippii** O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem **10**: 559. 1929.

Eudema trichocarpa Muschler, Bot. Jahrb. Syst. **40**: 276. 1908. = **Weberbauera trichocarpa** (Muschler) J. F. Macbr. Candollea **5**: 356. 1934.

ACKNOWLEDGMENTS

I am most grateful to Reed C. Rollins for his critical review of the manuscript and to Donald H. Pfister for obtaining funds from the Harvard University

Herbaria that supported the SEM portion of the research. Many thanks are due Elizabeth A. Shaw for correcting the Latin diagnoses, Trisha Rice for the SEM work, Barbara Nimblett for typing the manuscript, Gustavo Romero for his help with the Spanish, Michael A. Canoso for obtaining the loans, my wife, Mona, for her continuous support, and Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice. I am thankful to the directors and curators of the herbaria (abbreviations follow Holmgren *et al.,* 1981), who kindly sent the material for this study.

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MULTILACUNAR NODAL ANATOMY IN MYTILARIA (HAMAMELIDACEAE)[1]

A. Linn Bogle[2]

Multilacunar nodal anatomy associated with unique sheathing stipules in the genus *Mytilaria* (subfam. Exbucklandioideae) is reported for the first time in the Hamamelidaceae, a family usually characterized by trilacunar nodes. The number of gaps and traces ranged from eight to 12 in the nodes analyzed.

The significance of anatomical data from the stem-node-leaf continuum for systematic and phylogenetic studies is now generally recognized. The literature and the development of ideas in this field have been well reviewed by Howard (1979) and others (Carlquist, 1961; Radford *et al.*, 1974; Takhtajan, 1980). One of the major results of early studies of nodal anatomy in dicotyledons (Sinnott, 1914; Sinnott & Bailey, 1914) was the recognition of three major nodal types: trilacunar three-trace, unilacunar one-trace, and multilacunar multitrace. It was also established that the presence of stipules was usually correlated with trilacunar nodes, the absence of stipules with unilacunar nodes, and the presence of sheathing leaf bases or stipular structures with multilacunar nodes.

The purpose of this paper is to report the nodal structure of the unusual unistipulate leaves of the monotypic genus *Mytilaria* Lecomte. The nodes display a vascular pattern not previously known in the Hamamelidaceae but of apparent taxonomic significance.

In the Hamamelidaceae all of the approximately 30 currently recognized genera are stipulate. In most cases the stipules are paired, small, membranous, and ephemeral. However, the stipules of the three genera usually grouped in subfam. Exbucklandioideae are among the most unusual in the family. Those of *Exbucklandia* R. W. Brown and *Chunia* H. T. Chang are large, leathery, oblong to orbicular, and connate in the bud, completely enclosing the younger leaves and the shoot apex (Griffith, 1836; Lubbock, 1899; Chang, 1948). Their broadly attached bases leave a girdling scar at the node, imposing a jointed appearance on the stem. In contrast, the leaves of *Mytilaria laosensis* Lecomte are unique in the family in having a single, long, narrowly conical, sheathing stipule, which Lecomte (1924) thought consisted of two stipules united into a conical sheath. It attaches all the way around the stem, opens by a single

[1]This paper represents scientific contribution no. 1604 from the New Hampshire Agricultural Experiment Station.

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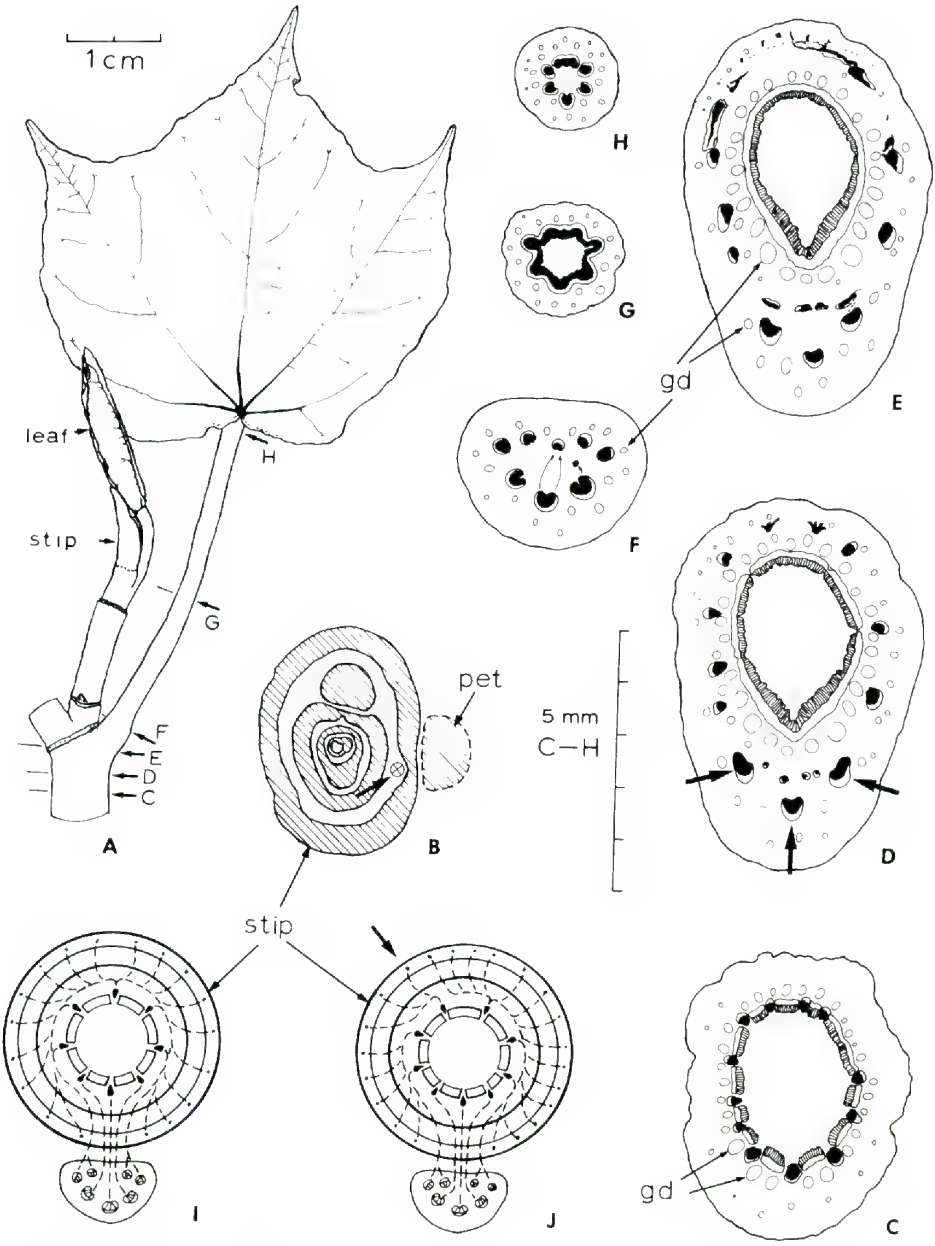
Journal of the Arnold Arboretum **71**: 111–118. January, 1990.



Nodal anatomy of *Mytilaria laosensis*: A, stem tip, showing young leaf prior to unfolding, with stipule still attached, and slightly older, expanding leaf with stipule scar at base (arrows indicate positions of sections in C–H); B, diagram of transverse section through bud, showing succession of 4 petiole–stipule sheath complexes in different stages of development (arrow indicates axillary bud; C, transverse section of internode, showing differentiation of 12 leaf traces (blank circles = gum ducts of ground tissue in C–H); D, transverse section of lower nodal area, showing 12 leaf traces in ground tissue, those farthest from leaf base beginning to branch (arrows indicate traces forming the 3 main abaxial bundles of petiole; remaining laterals contributing to petiole and/or stipule sheath); E, transverse section of upper nodal area, showing leaf base, part of stipule scar on side opposite leaf base, and horizontal course of some leaf traces on side of stem opposite

longitudinal suture that faces the petiole of the associated leaf, and at maturity is circumscissile caducous, also leaving the stem with a girdling scar and a jointed appearance (see FIGURE, A, B).

In general, anatomical data on the stem-node-leaf continuum in the Hamamelidaceae are fragmentary and scattered in a number of publications. Some of these studies (Sinnott, 1914; Sinnott & Bailey, 1914; Skvortsova, 1960; Bisht *et al.*, 1983) have emphasized the number of gaps in the stem stele and the number of traces departing from them to enter the leaf base. Others (Thouvenin, 1890; Morvillez, 1919; Tong, 1930; Chang, 1948; Covin, 1959; Skvortsova, 1960; Harjal *et al.*, 1984) have emphasized the number of vascular strands entering the leaf base (without reference to the structure of the node), the pattern formed by the vascular tissue at different levels in the petiole and midrib, and whether the vascular bundles are collateral or concentric in form. With regard to the subfamily Exbucklandioideae, several of these authors (Morvillez, 1919; Tong, 1930; Skvortsova, 1960) have included observations on the vascular structure of the petiole and midvein of one or another of the three genera of the subfamily in the context of broader studies of petiolar anatomy, but not on their nodal anatomy.

Among authors considering the anatomy of the node in the Hamamelidaceae, Sinnott (1914) described the Hamamelidaceae as being typically trilacunar. Sinnott and Bailey (1914, *pl. 44, fig. 4*) studied at length the origin of the vascular supply to the stipules, including those of *Hamamelis* L., which they designated (p. 453) as the "typical trilacunar dicotyledon," and indicated that in trilacunar nodes the stipular supply is typically derived from the lateral traces.

Skvortsova (1960, p. 126), as part of a broader study of petiole structure in the Hamamelidaceae and the Altingiaceae, investigated the nodal structure of leaves in which the vasculature "in the lower part of the petiole was established as an arc or semicircle" and concluded that a correlation existed between trilacunar nodal structure, three traces entering the leaf base, and a vascular pattern in the form of an arc or semicircle in the lower part of the petiole.

Bisht and colleagues (1983), on the other hand, reported unilacunar nodal structure for four genera of Hamamelidaceae (*Corylopsis* Sieb. & Zucc., *Distylium* Sieb. & Zucc., *Hamamelis, Parrotia* C. Meyer).

Among the authors who have concentrated on the vascular pattern of the petiole, Morvillez (1919, *fig. 5*) described three traces entering the leaf base in species of *Hamamelis, Parrotia, Fothergilla* L., and *Liquidambar* L. and implied a similar condition in *Disanthus* Maxim., *Exbucklandia* (as *Bucklandia*

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leaf base; F, transverse section through base of petiole, showing vascular cylinder of 8 bundles; G, transverse section at mid-level of petiole, bundles forming vascular cylinder; H, transverse section through top of petiole, vascular cylinder broken up into discrete bundles, each of which will form leaf vein; I, diagrammatic representation of vascular pattern in node with 8 gaps and traces (dashed lines indicate branching patterns of lateral traces supplying petiole and stipule sheath in I, J); J, diagrammatic representation of vascular pattern in node with 9 gaps and traces. (Abbreviations: gd = gum duct, pet = petiole, stip = stipule.)

R. Br.), and *Altingia* Noronha. He described the structure of the vascular system at different levels in the petiole and the derivation of the major leaf veins from the petiole vasculature.

Tong (1930) described the vascular condition in the lower and upper parts of the petiole and the base, middle, and tip of the midvein for 20 species of 14 genera of Hamamelidaceae, including *Exbucklandia* (as *Bucklandia*). He described three collateral bundles in the lower part of the petiole for 17 of the species, one collateral bundle in two species of *Fothergilla,* and one concentric bundle in the lower part of the petiole of *Exbucklandia,* this giving rise to three concentric and five collateral bundles in the upper part of the petiole.

Covin (1959, *fig. 6*) illustrated the petiole vasculature of *Mytilaria* as being "polystelic" at mid-petiole level, while at the base of the midvein it formed a "simple fold" in *Mytilaria* and a "simple arc" in *Exbucklandia* (as *Bucklandia*).

Skvortsova (1960) examined the petiolar vascular system at the low, middle, and high levels in 22 genera of the family, including *Exbucklandia* and *Mytilaria,* and emphasized the configuration of the vasculature at mid-level. She found that all genera except *Liquidambar, Altingia, Mytilaria,* and *Embolanthera* Merr. have a cylinder of vasculature at mid-level. *Mytilaria* is illustrated (*fig. 1-22*) as having four arcuate bundles and an adaxial vascular band at mid-level, in contrast to a complete vascular cylinder at that level in *Exbucklandia* (*fig. 1-16*).

Chang (1948, p. 67), in his description of the new genus *Chunia,* provided the only direct comparative data for all three genera of Exbucklandioideae, stating that in the petiole of *Chunia* the vascular tissue "unites into a cylinder with prominent ridges," while in *Exbucklandia* (as *Bucklandia*) it is "horseshoe shaped," and in *Mytilaria* it is "arranged in discrete bundles."

MATERIALS AND METHODS

The observations reported here are based on hand sections, clearings, and serial sections of young, alcohol-preserved nodes and buds of *Mytilaria laosensis* obtained from the Biological Laboratory-Factory, Zhaoqing Training College, Zhaoqing, Guangdong, People's Republic of China (no collection number or data provided); on herbarium specimens of *Chunia* (*Wang 36075,* NYBG); and on personal field collections of *Exbucklandia populnea* (Bogle *1379, 1387*). All voucher materials are on deposit in the Botany and Plant Pathology Department of the University of New Hampshire (NHA).

For clearing, young nodes were bleached in 5% NaOH, washed in tap water, and cleared in 5% chloral hydrate. Transverse sections of nodes and petioles were made by standard paraffin-embedding techniques and stained with safranin–fast green (Sass, 1958). Hand sections were stained with phloroglucinol–50% HCl and mounted in glycerine.

OBSERVATIONS

Transverse sections of a young bud of *Mytilaria laosensis* revealed a condensed series of concentric stipular sheaths with their associated petioles. A

single suture was seen as a thin area in the stipule sheath opposite the petiole. There was no evidence of a second suture on the opposite side of the sheath to support an interpretation of two stipules united into a conical sheath. The stipule sheath encloses the related axillary bud (see FIGURE, B, arrow).

In sections of the stem of *Mytilaria* taken below the node of a young leaf, a number of leaf traces and gaps were clearly differentiated (see FIGURE, C). The gaps were more or less equally spaced around the circumference of the vascular cylinder. The number of gaps and traces ranged from eight to 12 in the nodes examined (see FIGURE, C, I, J).

The three traces originating nearest the leaf base moved directly and independently into the leaf base to form the three major abaxial bundles of the petiole vascular system. The five to nine bundles originating farther around the stem from the leaf base bent toward the leaf and ran more or less horizontally around the stem in the ground tissue, toward the leaf base, often anastomosing with adjacent traces to form an incomplete vascular ring around the node. As many as 18 to 24 minor branches diverge from the horizontal traces to provide the vascular supply to the base of the sheathing stipule (see FIGURE, I, J).

The trace farthest from the leaf base bifurcates after leaving the gap, sending branches in each direction around the node, as well as to the stipule (see FIGURE, D, I, J). Occasionally a leaf trace provided traces to the stipule but not to the leaf base (see FIGURE, J, arrow).

In the base of the petiole, seven or eight major bundles were observed, sometimes accompanied by minor cortical strands (see FIGURE, F). The three large abaxial bundles were each derived from single leaf traces originating from the three gaps directly opposite the leaf base, as described above. The two larger bundles in each angle of the petiole cross section resulted from the branching of a single bundle derived on each side of the node from fusion of the horizontal trace system (see FIGURE, I, J). Additional, smaller bundles may appear on the adaxial side of the petiole vascular cylinder, or in the central ground tissue, as derivatives of minor branches of the major bundles (see FIGURE, F, arrows).

At mid-petiole level the major bundles of the petiole base had fused into a fluted vascular cylinder (see FIGURE, G), which continued almost to the tip of the petiole. Just prior to joining the blade, the vascular cylinder again broke up into distinct bundles, each of which formed one of the major veins of the palmately veined leaf (see FIGURE, H).

In contrast to the multilacunar nodal structure of *Mytilaria,* the nodes in my material of *Exbucklandia* exhibit trilacunar, three-trace structure, with vascular supply to the large stipules derived from the lateral traces.

DISCUSSION

Nodal anatomy is generally considered to be a conservative feature of plant structure and to be a useful character at various levels in phylogenetic and taxonomic studies. However, Carlquist (1961, p. 87) warned that nodal anatomy can vary within a single plant, and that "there is no single point along

the petiole that could be called 'characteristic' or 'typical,' or be used to the exclusion of other sections for comparative purposes."

With regard to the Hamamelidaceae, Sinnott (1914) listed the family as trilacunar, while Skvortsova (1960) reported trilacunar nodes in those taxa of the family in which the vascular pattern in the lower part of the petiole is arc shaped or semicircular. Unfortunately, Skvortsova did not comment on the nodal structure of those taxa having a different vascular pattern in the lower petiole, and neither author was able to study all genera of the family. My observations (unpublished) on the nodes of foliage leaves of various genera of Hamamelidaceae (*Altingia, Liquidambar, Rhodoleia* Champ., *Exbucklandia, Disanthus, Hamamelis, Eustigma* Gardner & Champ., *Corylopsis* Sieb. & Zucc., *Sinowilsonia* Hemsley, *Parrotia, Parrotiopsis* Schneider, *Distylium, Matudaea* Lundell) indicate that all have trilacunar, three-trace nodes.

There are, however, reports in the literature that present conflicting information. Bisht and colleagues (1983, *fig. 1*) reported unilacunar, one-trace nodes in *Distylium racemosum* Sieb. & Zucc., *Hamamelis japonica* Sieb. & Zucc., and *Hamamelis virginiana* L. (which Sinnott & Bailey, 1914, regarded as the typical trilacunar dicotyledon); unilacunar, three-trace nodes in *Parrotia persica* C. Meyer, and unilacunar, four-trace nodes in *Corylopsis spicata* Sieb. & Zucc. In contrast, Harjal and co-workers (1984, *table 2*), considering only the petiole vasculature, reported only one strand entering the petiole in *Corylopsis spicata, Distylium racemosum, Rhodoleia forrestii* Chun ex Exell, and *Trichocladus crinitis* Pers., as opposed to three in *Liquidambar styraciflua* L. and *Parrotiopsis jacquemontiana* Rehder. Thouvenin (1890), also considering only the petiole vasculature, reported three bundles departing from the stem (without reference to the number of lacunae) and entering the petiole in both *Trichocladus crinitis* and *T. elliptica* Ecklon & Zeyher.

Thus, several taxa (*Distylium racemosum, Hamamelis japonica, H. virginiana, Corylopsis spicata, Parrotia persica*) have been reported or observed to have either trilacunar, three-trace nodes, or unilacunar nodes with one, three, or four traces. These and other inconsistencies suggest the need for a more thorough and detailed study of the stem-node-leaf continuum in the Hamamelidaceae, particularly with regard to intraspecific variation.

Anatomical characters from the stem-node-leaf continuum have been used in some taxonomic studies regarding the relationships of genera and subfamilies in the Hamamelidaceae, including *Mytilaria* and *Exbucklandia*. Morvillez (1919) considered the similar petiolar structure in *Disanthus* (which now comprises subfam. Disanthoideae) and *Exbucklandia* (as *Bucklandia*, the two genera together then constituting tribe Bucklandieae) to be intermediate forms, linking the tribe Balsamiflueae (*Liquidambar* and *Altingia*, now subfam. Liquidambaroideae) to the remainder of the Hamamelidaceae. Skvortsova (1960), on the other hand, considered the data from petiole vascular structure to support the segregation of *Liquidambar* and *Altingia* as a family (Altingiaceae), to which she suggested that *Mytilaria* is related.

The distinctive vegetative morphology shared by *Exbucklandia, Chunia,* and *Mytilaria* makes them easily identifiable as the only members of subfam. Exbucklandioideae. However, the three genera differ significantly in floral morphology, and in recent years they have been separated by some authors into

two subfamilies. Chang (1973) segregated *Mytilaria* and *Chunia* in the new (and sixth) subfamily Mytilarioideae, leaving only *Exbucklandia* in the Exbucklandioideae. Huang and Lee (1982) supported this segregation on the basis of wood anatomy, suggesting a closer relationship of the Mytilarioideae to subfam. Disanthoideae than to any of the other subfamilies (i.e., Liquidambaroideae, Rhodoleioideae, Hamamelidoideae). Takhtajan (1980), on the other hand, listed subfam. Chunioideae (rather than Mytilarioideae) as one of six subfamilies in the Hamamelidaceae but did not indicate which of the three genera of Exbucklandioideae he would assign to it or his reasons for removing them from the Exbucklandioideae.

Mytilaria is clearly set apart from the other two genera of Exbucklandioideae by its single, conical, sheathing stipules; its gum ducts (secretory canals) in the ground tissue throughout the plant, including the flowers; its numerous, complete flowers with nearly inferior ovaries sunken in a long, fleshy spike; its petals and stamen filaments fused basally into a short tube; and its ten stamens with horned filaments surmounted by hooded anthers, connivent in a cycle over minute styles and stigmas. The presence of multilacunar nodes in *Mytilaria,* as opposed to trilacunar nodes and paired stipules in *Exbucklandia,* adds yet another distinctive character to this list, suggesting that separation of *Mytilaria* from *Exbucklandia* is more appropriate at the tribal level within subfam. Exbucklandioideae than as the separate subfam. Mytilarioideae.

The position of *Chunia* in such a subdivision of the Exbucklandioideae is as yet uncertain. Its floral morphology is distinctive (naked, bisexual flowers sunken in a relatively-few-flowered, short spike) and is perhaps closer to that of *Exbucklandia* than that of *Mytilaria.* It also shares paired, connate stipules with *Exbucklandia.* However, my preliminary observations on the few nodes available for study indicate that it, too, has multilacunar nodes. This would tend to emphasize the unity of the three genera as a single subfamily. At the same time, it could be taken as support for the taxonomic separation of *Mytilaria* and *Chunia* from *Exbucklandia,* as proposed by Chang (1973). However, the significant differences in floral morphology between *Mytilaria* and *Chunia* may militate against their being paired in this way. Investigation is continuing on *Chunia.*

ACKNOWLEDGMENTS

I wish to express thanks to the directors of the Harvard University Herbaria, the Museum of Natural History, Paris, and the New York Botanical Garden for access to or loans of specimens of *Chunia, Exbucklandia,* and *Mytilaria.* I am also deeply grateful to Shiu-ying Hu for translating the Chinese literature, and to Richard A. Howard for reviewing the original manuscript.

Financial support from the University of New Hampshire Central University Research Fund, grant no. 980, is gratefully acknowledged.

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ADDITIONS TO THE FLORA OF CHINA

DAVID E. BOUFFORD,[1] ZHAN-HUO TSI,[2] AND PEISHAN WANG[3]

Four taxa, *Dryopteris kweichowicola* (Dryopteridaceae), *Gastrochilus nanus* (Orchidaceae), *Rubus fanjingshanensis* (Rosaceae), and *Sabia swinhoei* var. *parvifolia* (Sabiaceae), are described as new. *Deinostema adenocaulon* is reported for the first time from China and represents a disjunction of ca. 1800 km from the closest populations in Korea.

Joint fieldwork in northeastern Guizhou Province, China, in 1986 by Chinese and American botanists resulted in the collection of 2474 numbers and 28,633 sheets of flowering plants and ferns, including four previously undescribed taxa, *Dryopteris kweichowicola* Ching ex P. S. Wang (Dryopteridaceae), *Gastrochilus nanus* Z. H. Tsi (Orchidaceae), *Rubus fanjingshanensis* L. T. Lu (Rosaceae), and *Sabia swinhoei* Hemsley ex Forbes & Hemsley var. *parvifolia* Y. H. Xiang & Q. H. Chen (Sabiaceae), and one, *Deinostema adenocaulon* (Maxim.) Yamaz. (Scrophulariaceae), previously unknown in China. The collections are all from the vicinity of the 38,000-hectare Fanjing Shan Nature Reserve, one of six Man and the Biosphere reserves in China (Chen, 1988). The reserve contains rich botanical resources in associations ranging from broad-leaved evergreen forests at the lowest elevations (ca. 550 m) through mixed deciduous–broad-leaved evergreen forests at middle elevations to subalpine scrub and meadows and dwarf bamboo thickets near the summits of the highest peaks at ca. 2550 m (Huang *et al.*, 1982). The area, an island of relatively undisturbed vegetation, is unusual within the vast, mostly deforested south-central part of China because of the richness of its flora.

Dryopteris kweichowicola Ching ex P. S. Wang, sp. nov. FIGURE 1.

Affinis Dryopteris wallichianae (Sprengel) Hylander, sed minore, folliis tenuiter chartaceis, soris prope marginem, venis utrinque facie conspicuis.

Plants 50–70 cm tall. Rhizome short, erect. Fronds tufted, thin-chartaceous, the upper surface nearly glabrous, with few hairlike scales along costa, the lower surface with ovate-lanceolate scales; stipe 13–16 cm long, 3–5 mm in diameter, clothed in dense, brown scales, those at stipe base entire and those above

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Journal of the Arnold Arboretum **71**: 119–127. January, 1990.

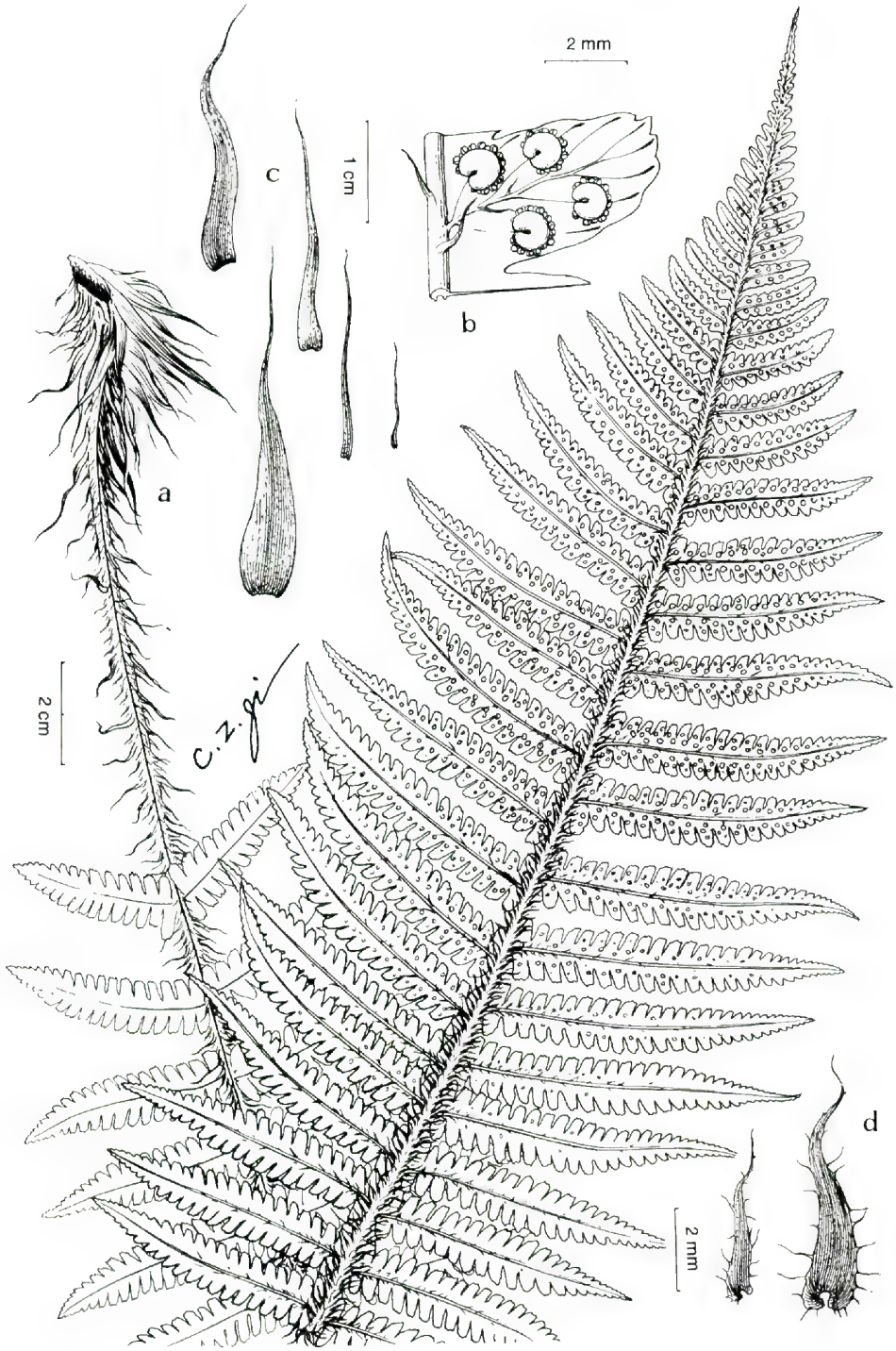

FIGURE 1. *Dryopteris kweichowicola*: a, frond; b, pinnule; c, scales from rhizome; d, scales from stipe.

fimbriate; leaf blade lanceolate, 35–50 cm long, 12–15 cm wide, gradually narrowed toward base, acuminate at apex, bipinnate; pinnae 25 to 30 pairs, patent, the lowest ones slightly reflexed and much shortened, the middle ones lanceolate, 7–8 cm long, 1–1.3 cm wide, sessile, with base truncate, apex short-acuminate, pinnule segments ca. 20 pairs (these patent, oblong, ca. 5–6 mm long, 2–3 mm wide, the apex blunt, with 3 to 5 teeth, the veins 4- to 6-jugate, oblique, simple or forked). Sori 2 to 4 pairs per segment near margin; indusium brown, persistent.

TYPE. China, Guizhou Province, Jiangkou Xian, vicinity of Jinding along the crest of the Fanjing Shan mountain range, elev. ca. 2200 m, growing at base of old wall in moist situation, 27 August 1986, *Sino-Amer. Guizhou Bot. Exped. 451* (holotype, PE; isotypes, A, CAS, HGAS, TI).

ADDITIONAL SPECIMENS EXAMINED. **China.** GUIZHOU PROVINCE: without further locality, *S. W. Teng 51367* (PE), *51368* (PE); Jiangkou Xian, by small stream, 1700 m alt., *Z. S. Zhang et al. 402211* (PE).

This species is very similar to *Dryopteris wallichiana* in the shape of the fronds. The essential difference between the two is in the position of the sori: in the former they are near the margins of the segments, while in the latter they are near the costae.

Gastrochilus nanus Z. H. Tsi, sp. nov. FIGURE 2.

Species Gastrochilus toramani (Makino) Schltr. et G. raraensis Fukuyama affinis, ab illis floribus sine punctis purpureis; forma epichilii et petalorum; hypochilo cylindrico-subcylindrico differt.

Epiphytic. Stems creeping, 3–4 cm long, with thick and slightly flexed roots. Leaves many, distichous, alternate, closely arranged, spreading, somewhat fleshy, elliptic-oblong, 8–10 mm long, 5–6 mm wide, apex acute, base jointed to sheaths, green with purple spots on both surfaces. Inflorescence leaf opposed, suberect-patent, 6–11 mm long, bearing 5 or 6 subumbellately arranged flowers; peduncle slightly fleshy, gradually thickened from base to apex, with tubular sheath near base; floral bracts with purple spots, somewhat fleshy, ovate-triangular, ca. 1–1.3 mm long, apex acute; ovary greenish, 4–5 mm long, slightly angled; flowers spreading, greenish; sepals and petals somewhat fleshy, apex obtuse, 1-veined; dorsal sepal elliptic, concave, 2.2 mm long, 1.2 mm wide, the lateral pair ± oblique-oblong, as long as dorsal one; petals oblong, smaller than sepals; labellum adnate to lower half of column, obscurely 3-lobed; lateral lobes of hypochile small, suberect, triangular, villous internally; epichile membranous, patent, reniform, ca. 2 mm long, 2.5 mm wide at base, subtruncate, apex notched, edge and upper surface densely pubescent, with olivaceous, thickened patch in disc; spur straight, nearly parallel to pedicel, cylindrical, 2.8–3 mm long, ca. 1 mm broad, ± contracted in middle, apex broadly rounded; column thick, ca. 0.5 mm long; anther hemispherical, abruptly contracted into triangular, acute apex; rostellum bifid; pollinia 2, globose, attached by linear caudicle to incrassate, oblong, apically bifid gland.

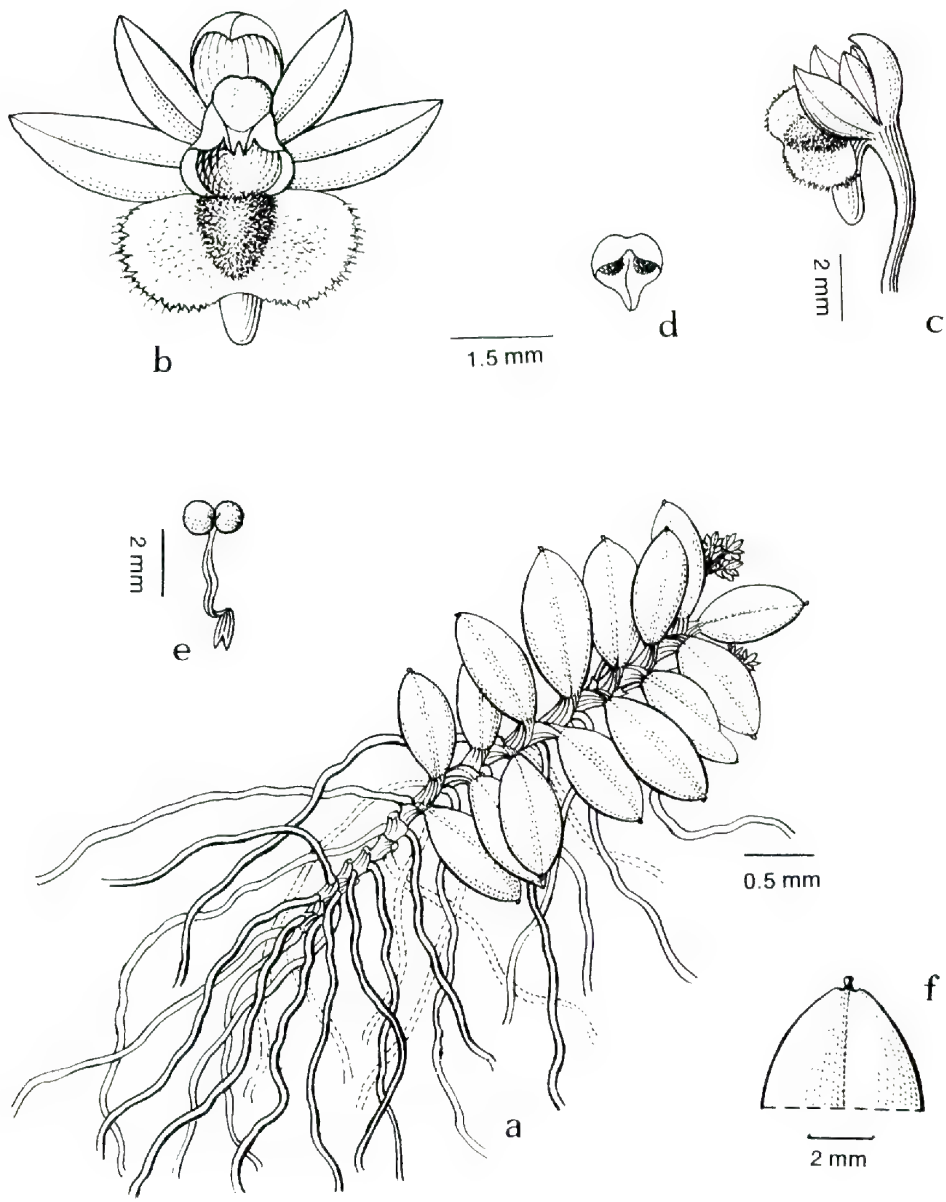

FIGURE 2. *Gastrochilus nanus*: a, habit; b, flower, front view; c, flower, side view; d, operculum; e, stipe; f, leaf tip.

TYPE. China, Guizhou Province, Jiankou Xian, Yuao, in the valley of the Heiwan River, elevation ca. 1000 m, 26 August 1986, *Sino-Amer. Guizhou Bot. Exped. 407* (holotype, PE; isotypes, A, HGAS).

Gastrochilus nanus is allied to *G. toramanus* and *G. raraensis,* but it differs from the former in having a reniform epichile and oblong petals and from the

latter in having smaller greenish flowers with a cylindrical to subcylindrical, vertical hypochile and differently shaped petals.

Rubus fanjingshanensis L. T. Lu, sp. nov. FIGURE 3.

Species ab R. treutleri J. D. Hooker, foliis 3–5-lobatis, lobis terminalibus apice acutis, lateralibus obtusis, margine irregulariter grosse-serratis; stipulis angustioribus, 10–15 mm longis, palmatis partitis, lobis linearibus vel linearilanceolatis, sepalis internis late-ovatis vel ovato-lanceolatis; externis foliolis, margine dissectis, lobulis lanceolatis, differt.

Small, trailing shrub; branches terete, the older ones dark brown, the young shoots brown or brownish, villous, with thin acicular prickles slightly dilated at base intermixed with stipitate glands. Stipules free, 1.4–1.8 cm long, 1–1.4 cm wide, villous and glandular-hairy on both surfaces, palmately parted, the lobes lanceolate or triangular-lanceolate, 3–7 mm long, 1.3–3 mm wide. Leaves with petiole 4–8 cm long, long-hairy and with acicular prickles and stipitate glands intermixed; blade orbicular or nearly orbicular, 7–11 cm long, 6.5–11 cm wide, 5- (rarely 7-)lobed, the lobes obtuse to rounded with terminal one slightly longer than or equal to lateral ones, base deeply cordate, margins irregularly serrulate, apex obtuse, upper surface dark green, lower surface paler, both surfaces adpressed-villous but lower surface more densely so, veins glabrescent and sparsely hairy at maturity, midrib and lateral veins on lower surface with acicular prickles and sometimes also sparse stipitate glands. Inflorescences and flowers not seen; infructescences terminal short racemes, 4–5 cm long, or fascicles in axils of the leaves; rachises, fruiting pedicels, and calyces covered with long hairs and acicular prickles, sometimes with sparse stipitate glands intermixed; fruiting pedicels 8–11 mm long; bracts resembling stipules, but smaller; calyx cup shaped; sepals 5, broadly ovate-lanceolate to oblong-ovate, 8–14 mm long, 4–6 mm wide, the outer ones usually wider, dissected at apex or in upper part, with lobes linear to linear-lanceolate, 2–5 mm long, 1–1.5 mm wide, apex caudate; persistent stamens numerous, 3–4 mm long, filaments somewhat broadened at base, anthers globose or short-oblong; persistent pistils numerous, glabrous; torus elevated, long-hairy. Fruits aggregates consisting of many united drupelets, subglobose, 7–10 mm in diameter, red, glabrous, crowned with persistent calyx; stones subreniform, 1.5–2.5 mm long, 1–1.8 mm wide, distinctly rugose. Fruiting in August and September.

TYPE. China, Guizhou Province, Jiangkou Xian, vicinity of Jinding along the crest of the Fanjing Shan mountain range, elev. 2000–2300 m, 28–29 August 1986, *Sino-Amer. Guizhou Bot. Exped. 634* (holotype, PE; isotypes, A, CAS, HGAS, TI).

Rubus fanjingshanensis is apparently related to *R. treutleri,* but the latter differs markedly in having leaves 3- to 5-lobed, with the terminal lobe acute at the apex, the lateral ones obtuse, and the margins irregularly and minutely serrate; narrower, fimbriate stipules 10–15 mm long, with linear to linear-lanceolate lobes; and sepals ovate to ovate-lanceolate, the outer ones foliose and dissected with lanceolate lobes.

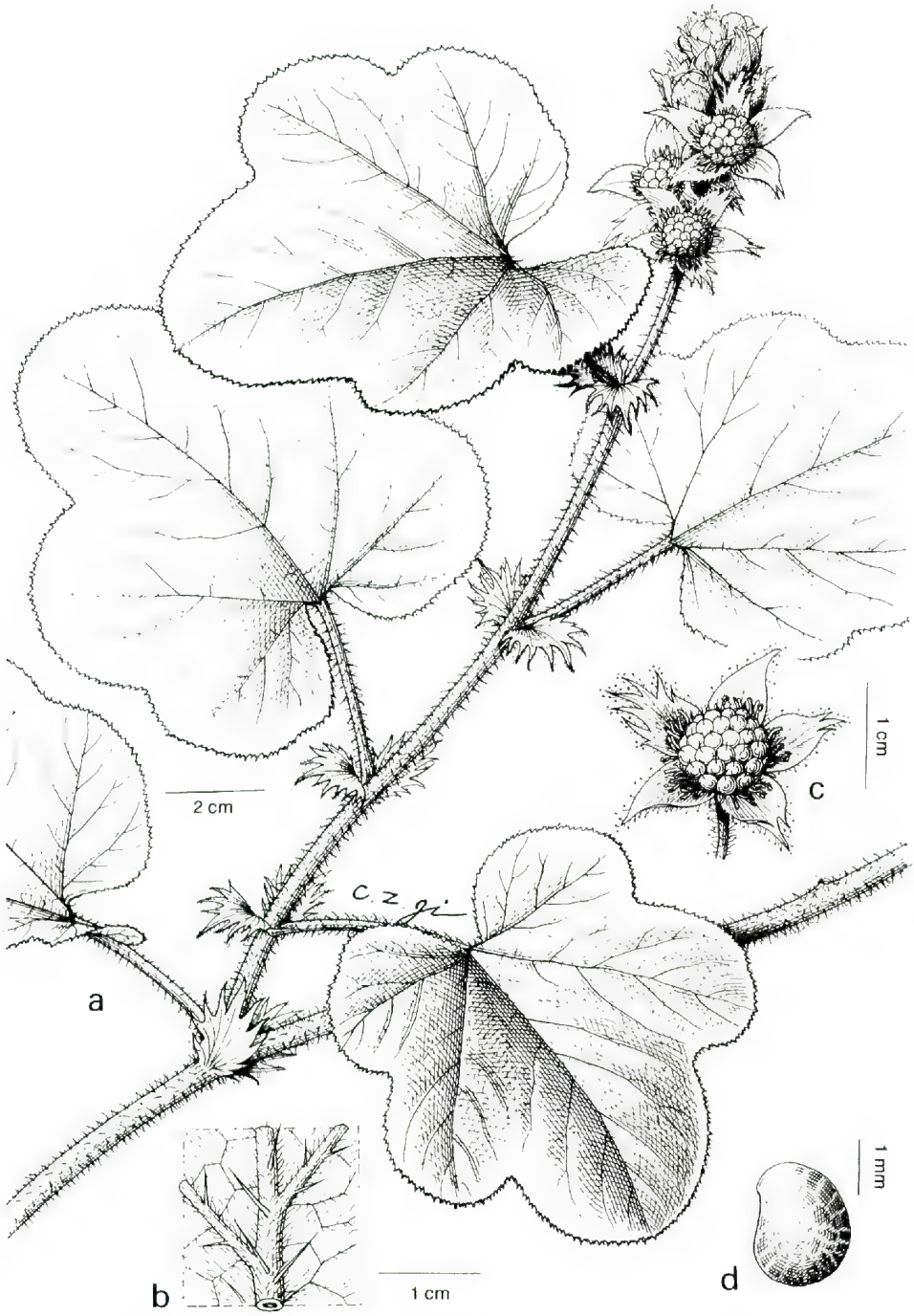

FIGURE 3. *Rubus fanjingshanensis*: a, upper portion of branch; b, lower leaf surface; c, fruit; d, seed.

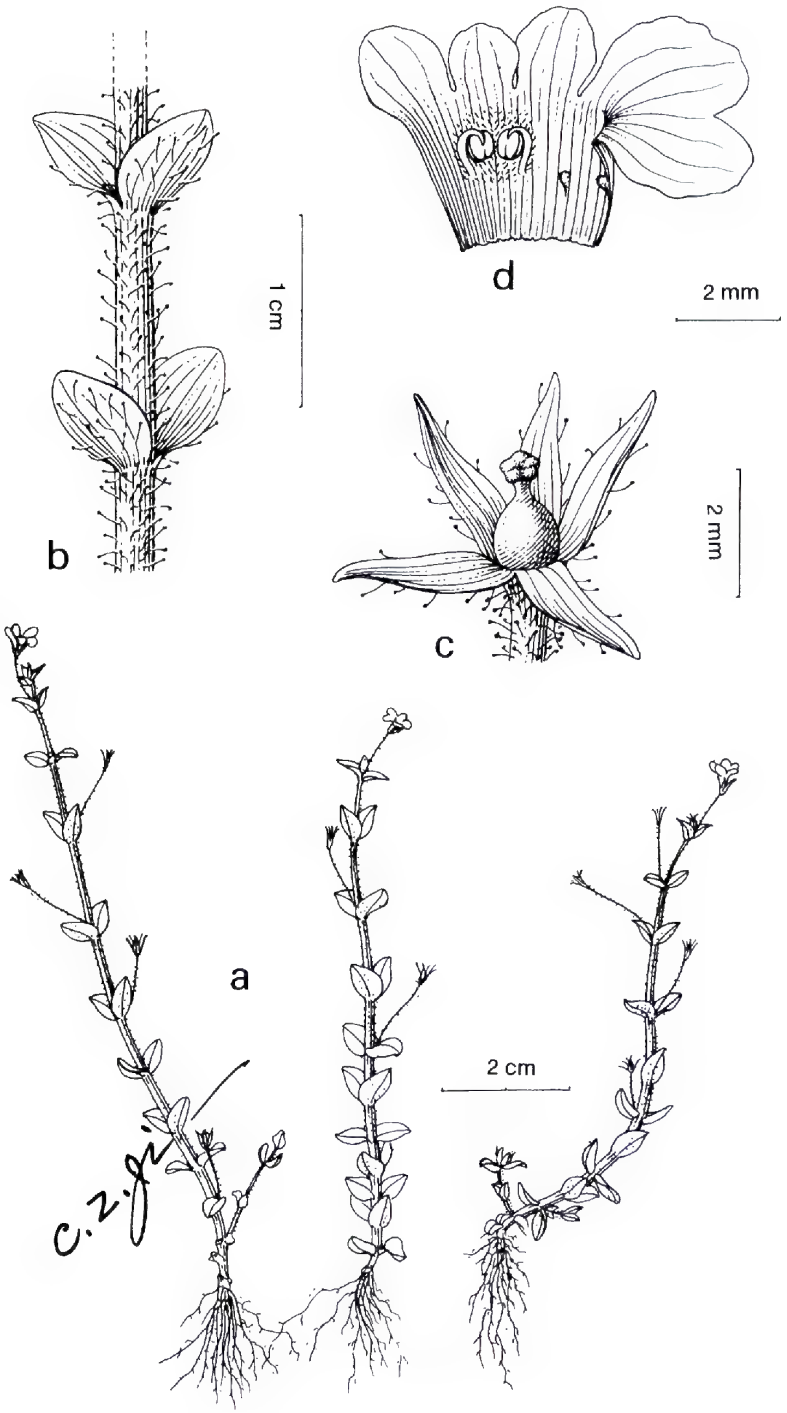

FIGURE 4. *Deinostema adenocaulon*: a, habit; b, portion of stem showing glandular hairs; c, immature capsule; d, flower opened to show attachment of stamens and callosities on inner surface of corolla tube.

Sabia swinhoei Hemsley ex Forbes & Hemsley var. **parvifolia** Y. H. Xiang & Q. H. Chen, var. nov.

A typo pedunculis pedicellisque brevioribus, 2–3 mm longis, foliis minoribus, 3–5 cm longis, 1–1.8 cm latis differt.

Leaves ovate or elliptic to sublanceolate, 3–5 cm long, 1–1.8 cm wide, base acute to subrounded, apex acute to acuminate, upper surface glabrous except for pubescent midrib, lower surface ± lax-pubescent, lateral nerves 5 to 7 pairs; petiole 2–3 mm long, densely pubescent. Cymes solitary, axillary; peduncles 3 mm long; pedicels 2 mm long. Drupelets obovoid-compressed, turning red at maturity.

TYPE. China, Guizhou Province, Jiangkou Xian, Daiyenpeng along the Kaitu River on SW side of Fanjing Shan mountain range, elevation ca. 800 m, *Sino-Amer. Guizhou Bot. Exped. 1082* (holotype, HGAS; isotypes, A, CAS, PE).

The variety differs from the typical one in having much shorter cymes and smaller leaves.

Deinostema adenocaulon (Maxim.) Yamaz. FIGURE 4.

Deinostema Yamaz., separated from *Gratiola* L., in which it was once placed, by its ebracteolate calyx, valvate (vs. imbricate) calyx lobes in bud, and pilose (vs. glabrous) anthers (Ohwi, 1965), and from *Dopatrium* Hamilton ex Bentham by its bilocular (vs. unilocular) ovary (Yamazaki, 1953), is a genus of two species restricted to wet places in eastern Asia. The most widespread species, *Deinostema violacea* (Maxim.) Yamaz., ranges from Honshu, Shikoku, Kyushu, and the Ryukyu Islands in Japan, as well as Korea (Ohwi, 1965) and the northeastern provinces of China, to Jiangsu on the Asian mainland (Hong, 1979). *Deinostema adenocaulon* was previously known from only Honshu, Shikoku, and Kyushu in Japan and from Cheju-do at the southern tip of the Korean peninsula (Ohwi, 1965; Park, 1974). The specimens from northeastern Guizhou, Jiangkou Xian, SE side of the Fanjing Shan mountain range along the Heiwan River in the vicinity of the Ecology Station of the Guizhou Academy of Sciences, 30 August 1986, *Sino-Amer. Guizhou Bot. Exped. 598* (A, CAS, GIB, PE, TI), were collected approximately 1800 km from the nearest previously known populations in Korea. In Guizhou the plants were abundant in a fallow paddy field with *Microcarpaea minima* (Konig) Merr., *Eleocharis congesta* D. Don, *Eriocaulon sieboldianum* Sieb. & Zucc., and *Rotala mexicana* Champ. & Schldl.

ACKNOWLEDGMENTS

We wish to thank Bruce Bartholomew and Stephen A. Spongberg, of the United States, and Qianhai Chen, Sizhao Fang, Jin-gen Qi, Yuling Tu, Yinghai Xiang, and Tsun-shen Ying, of China, all of whom participated in the fieldwork in northeastern Guizhou Province, China, in 1986, and Gustavo Romero and Rolla Tryon for reviewing the manuscript. We are particularly grateful to the

National Geographic Society, the Chinese Academy of Sciences, the Institute of Botany, Beijing, the Guizhou Academy of Sciences, and the Institute of Biology of Guizhou for their financial support of the fieldwork.

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A NEW VARIETY OF LYONIA (ERICACEAE) FROM PUERTO RICO

WALTER S. JUDD[1]

Lyonia truncata var. *proctorii* is a member of *Lyonia* sect. *Lyonia* and as such is characterized by an indumentum of unicellular hairs and multicellular, ferrugineous, biseriate-stalked, peltate scales. It is described and illustrated from specimens collected in the Sierra Bermeja of southwestern Puerto Rico. The new taxon is a member of the *Lyonia microcarpa–L. truncata–L. heptamera* evolutionary line. It is considered conspecific with *L. truncata,* a species previously considered endemic to Hispaniola. Thus, two species of *Lyonia* are now known from Puerto Rico: *L. rubiginosa* var. *stahlii* and *L. truncata* var. *proctorii.* Both taxa have their closest relatives in the mountains of central and southern Hispaniola.

The genus *Lyonia* Nutt. (Ericaceae subfam. Vaccinioideae tribe Andromedeae; see Judd, 1979, 1981) comprises 35 species (51 taxa[2]), of which 27 belong to sect. *Lyonia* (Judd, 1981). This section is characterized by its indumentum of multicellular, ferrugineous, biseriate-stalked, peltate scales. The group is most diverse in the Greater Antilles, where 24 species occur: 12 species (16 taxa) in Cuba; ten species (11) in Hispaniola; two in Jamaica; two in Puerto Rico (including the one described herein); and one in St. Thomas. Most species occur in montane communities (usually cloud forests or pinelands) and are restricted to a single island or mountain range.

Recent fieldwork in the Sierra Bermeja of Puerto Rico has resulted in the discovery of an undescribed variety of *Lyonia truncata.* This variety, described and illustrated here, brings the number of species and varieties recognized in the genus to 52.

Terminology used in the description follows Judd (1981).

Lyonia truncata Urban var. **proctorii** Judd, sp. nov. FIGURE.

Varietas haec a Lyonia truncata Urban varietatibus truncata et montecristina (Urban et E. Ekman) Judd differt in pedicellis 2–5 mm longis (vs. 2.5–10(–13) mm longis), corollis urceolatis/cylindraceis, 3–4.5(–5) mm longis (vs. ± cylindraceis, 4–7 mm longis), antheris 0.7–1 mm longis (vs. 1–1.5 mm longis), et capsulis 3–4.5 mm longis (vs. (3–)4–6.5 mm longis).

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[2]The recently described *Lyonia lippoldii* Berazaín & Bisse (Berazaín, 1987) is considered conspecific with *L. obtusa* (Judd, in prep.). In addition, recent field studies have indicated that *Lyonia obtusa* Griseb. var. *longipes* (Urban) Judd (see Judd, 1981) is best considered to be specifically distinct from *L. obtusa* (Borhidi, 1983; Berazaín, 1985).

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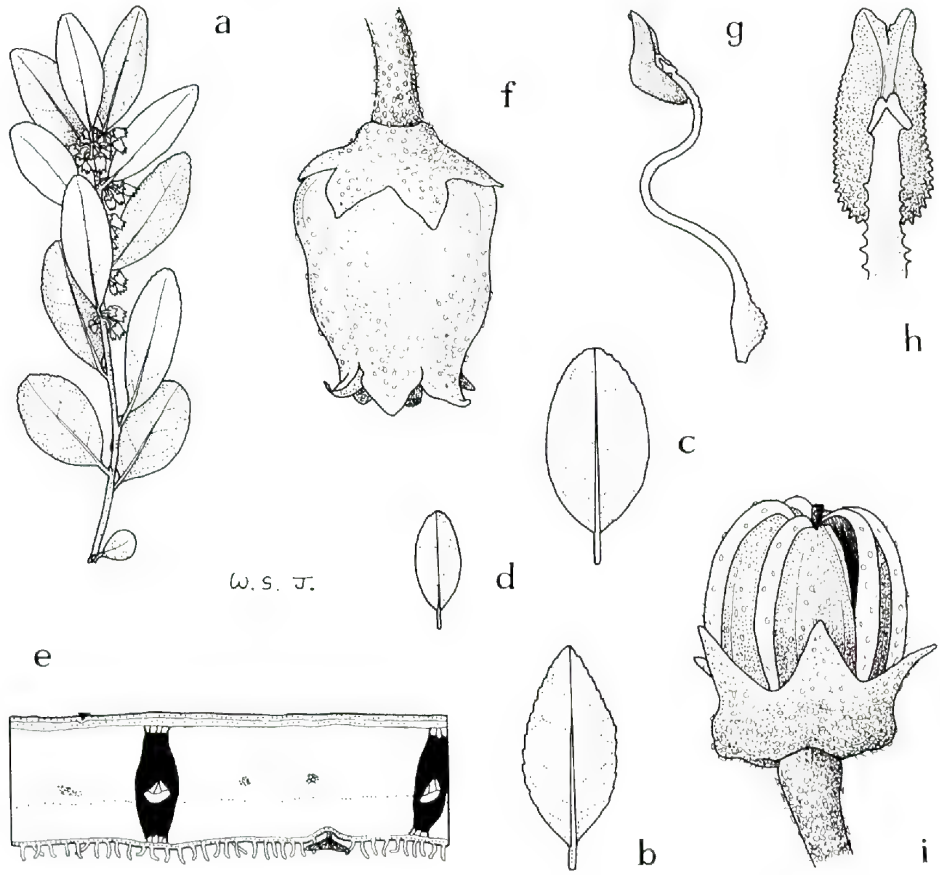
Journal of the Arnold Arboretum **71:** 129–133. January, 1990.



Lyonia truncata var. *proctorii* (from *Proctor & McKenzie 44010*): a, habit, × 0.5; b–d, leaves, × 0.5; e, cross section of leaf blade, × 50; f, flower, × 6; g, stamen, × 12.5; h, anther, × 25; i, capsule, × 6.

Evergreen erect shrub to ca. 1.5 m tall. Leaves with petiole 2–6.5 mm long; blade elliptic to ovate, 0.9–4.5 by 0.4–2.3 cm, ± flat, coriaceous, 0.25–0.3 mm thick, the margin plane to slightly revolute toward petiole, distal portion clearly to obscurely and irregularly toothed to entire, proximal portion entire to ± obscurely toothed, the abaxial surface sparsely to moderately lepidote, moderately to densely unicellular-pubescent. Inflorescences fasciculate, ca. 2- to 15-flowered; pedicels 2–5 mm long, sparsely pubescent; bracteoles opposite or subopposite, nearly basal to positioned on proximal ⅓ of pedicel, narrowly triangular, 0.9–2 mm long; bracts to ca. 2 mm long. Flowers 5- (or 6-)merous; calyx lobes triangular, 0.7–1.6 by 0.4–0.9 mm, the apex acuminate to acute, the abaxial surface lepidote, glabrous to densely pubescent (near base); corolla urceolate-cylindrical, 3–4.5(–5) by 2–3(–3.5) mm, white or sometimes slightly pink-tinged near mouth; filaments roughened, 2.5–3.5 mm long, unappendaged, anthers 0.7–1 mm long. Capsules ovoid, 3–4.5 by 2.5–4 mm, very sparsely pubescent, especially near base; seeds ca. 2.5 mm long.

TYPE. Puerto Rico, município de Cabo Rojo, Sierra Bermeja, Barrio Llanos Costa, upper slopes and summit of Cerro Mariquita, elev. 250–301 m, 11 October 1987, *G. R. Proctor & P. McKenzie 44010* (holotype, FLAS; isotypes, Herbarium, Dept. of Natural Resources, Puerta de Tierra, Puerto Rico (2 sheets)).

ETYMOLOGY. The varietal epithet honors George R. Proctor (b. 1920), of the Department of Natural Resources, Puerta de Tierra, Puerto Rico, who collected the herbarium material and sent it to me for identification as possibly representing an undescribed taxon.

LEAF ANATOMY.[3] Adaxial epidermis with inner periclinal walls lignified but not strongly thickened, height/breadth quotient of cells 0.5–1; adaxial hypodermis unilayered; lignified cells surrounding major veins transcurrent; mesophyll cells not lignified; stalk of peltate scales sunken into abaxial epidermis; petiole bundle bifacial, usually forming a cylinder.

DISTRIBUTION AND ECOLOGY. *Lyonia truncata* var. *proctorii* has been collected only on the upper slopes and summit of Cerro Mariquita of the Sierra Bermeja in southwestern Puerto Rico (município de Cabo Rojo), where it is locally common on exposed rocky slopes. The region is occupied by dry rocky scrub to low forest on Upper Jurassic to Lower Cretaceous chert. According to Proctor (pers. comm.), immediately associated species include *Acacia farnesiana* (L.) Willd., *Argythamnia candicans* Sw., *Aristida portoricensis* Pilger, *Bumelia obovata* (Lam.) A. DC., *Calliandra portoricensis* (Jacq.) Bentham, *Chamaesyce articulata* (Aublet) Britton, *Clusia rosea* Jacq., *Coccoloba microstachya* Willd., *Crossopetalum rhacoma* Crantz, *Digitaria eggersii* (Hackel) Henrard (new to Puerto Rico), *Eugenia sessiliflora* Vahl, *E. woodburyana* Alain, *Guettarda scabra* (L.) Vent., *Heteropteris purpurea* (L.) Kunth, *Lippia micromera* var. *helleri* (Britton) Moldenke, *Machaonia portoricensis* Baillon, *Melocactus intortus* (Miller) Urban, *Opuntia repens* Bello, *Ouratea littoralis* Urban, *Plumeria alba* L., *Polygala penaea* L., *Rheedia mariquitensis* Proctor, ined., *Sida jamaicensis* L. (new to Puerto Rico), *Stylosanthes viscosa* Sw. (new to Puerto Rico), *Tetramicra canaliculata* (Aublet) Urban, *Thrinax morrisii* H. A. Wendl., *Vernonia proctorii* Urbatsch, ined., and *Xylosma buxifolia* A. Gray. Flowering specimens of var. *proctorii* have been collected in October.

The Sierra Bermeja plants possess the synapomorphies (stamens lacking or with only minute spurs, and leaves at least sometimes strongly and irregularly toothed) delimiting a clade containing all previously recognized Hispaniolan and Puerto Rican species of *Lyonia* (Judd, 1981), as well as those (leaves densely unicellular-pubescent abaxially, with nonacuminate apices) characterizing a Hispaniolan clade called the "*Lyonia microcarpa–L. truncata–L. heptamera* evolutionary line" (Judd, 1981). However, they lack the apomorphies of the more derived members of this "evolutionary line" (see Judd, 1981, for characters involved).

[3]Techniques as in Judd, 1981.

The Sierra Bermeja plants are phenetically very similar to *Lyonia truncata,* a phenetically primitive, cladistically basal, metaphyletic species of the Hispaniolan clade, as can be seen by comparing the description given above with that of *L. truncata* (Judd, 1981). The leaves of both are characterized by moderate to dense unicellular indumentum abaxially, secondary veins not much more prominent than the tertiary, higher-order veins not forming a raised-reticulate network on the abaxial surface, inner periclinal walls of the adaxial epidermis lignified but not thicker than other epidermal walls, and peltate scales with their stalks sunken into the abaxial leaf epidermis. The Sierra Bermeja plants differ from *L. truncata* only in their shorter pedicels and their smaller flowers and capsules. The two are similar in habitat preference and in the low elevations they inhabit; they are nearly identical anatomically. Although individual features show overlap, plants of the two islands can be separated consistently by the characters in the diagnosis and the key. The Sierra Bermeja plants are believed distinctive enough to warrant taxonomic recognition and are considered to be a geographically isolated variety, *L. truncata* var. *proctorii.* Varietal rank has been preferred over specific recognition for this entity due to its strong phenetic similarity to *L. truncata* in both vegetative and reproductive features. *Lyonia truncata* occurs at lower elevations (100–1600 m) than any other Hispaniolan species of *Lyonia,* and it is perhaps not surprising that this recently discovered low-elevation population of *Lyonia* in Puerto Rico is best placed in *L. truncata.*

In 1981 I considered *Lyonia truncata* to be composed of two geographic varieties (equivalent to subspecies of many authors; see Borhidi, 1983) that differ in leaf size, orientation, and curvature (see Judd, 1981). *Lyonia truncata,* as now circumscribed, comprises three varieties, which can be distinguished as follows:

1. Corollas 3–4.5(–5) mm long, urceolate-cylindrical; anthers 0.7–1 mm long; pedicels 2–5 mm long; capsules 3–4.5 mm long; [Sierra Bermeja, Puerto Rico]. ..... var. *proctorii* Judd.
1. Corollas 4–7 mm long, ± cylindrical; anthers 1–1.5 mm long; pedicels 2.5–10(–13) mm long; capsules (3–)4–6.5 mm long; [Hispaniola].
   2. Leaves 0.8–3.5(–4) cm long, slightly concave to ± flat, sometimes slightly recurved; shrub to 2.5(–3) m tall, often densely branched; [Sierra de Baoruco and Massif de la Selle]. ..... var. *truncata.*
   2. Leaves (2.5–)3–5(–6.8) cm long, ± flat to recurved; shrub to small tree to 3–7 m tall, with branches more open; [Cordillera Central and Massif du Nord]. ..... var. *montecristina* (Urban & E. Ekman) Judd.

A second species, *Lyonia rubiginosa* (Pers.) G. Don var. *stahlii* (Urban) Judd, occurs on Puerto Rico in cloud forests at high elevations in the Cordillera Central and a few outlying localities (Judd, 1981). This species is easily distinguished from *L. truncata* var. *proctorii* in having leaves that completely lack unicellular hairs on the abaxial surface (Judd, 1981). It is noteworthy that *L. rubiginosa* and *L. truncata,* occurring on Hispaniola and Puerto Rico, are the only two members of sect. *Lyonia* that occur on more than one Antillean island.

ACKNOWLEDGMENTS

I thank George R. Proctor, who has collected this interesting *Lyonia* and has increased our knowledge of several other species of the genus through his numerous Antillean collections. I am also grateful to George Diggs and Peter Stevens for their helpful comments on a manuscript version of this paper.

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MENONVILLEA ROLLINSII (BRASSICACEAE), A NEW SHRUBBY SPECIES FROM CHILE

IHSAN A. AL-SHEHBAZ[1] AND CLODOMIRO MARTICORENA[2]

Menonvillea rollinsii, a new species described from northern Chile, is unique in the genus because of its shrubby habit and the development of cork in older stems.

Menonvillea DC. is a genus of thirty species distributed primarily in the drier portions of northern and central Chile and the adjacent provinces of Argentina. The range of the genus extends southward into Patagonia, and of the eight species that grow there, only *M. nordenskjoeldii* (Dusén) Rollins reaches as far south as Prov. Santa Cruz, Argentina, and Región Magallanes y Antártica Chilena (Boelcke & Romanczuk, 1984). Seventeen species are restricted to Chile and eight to Argentina, while five grow in both countries (Rollins, 1955).

Most species of *Menonvillea* are perennials with either an unbranched caudex or a deep, fleshy or woody, much-branched, rhizomelike caudex. About eight species are annuals, and two others, *M. linearis* DC. and *M. pinnatifida* Barnéoud, are annuals that sometimes perennate under favorable conditions. From the underground caudex, all of the perennial species annually produce new herbaceous stems that bear flowers and fruits and then die at the end of the growing season. None of the previously recognized species has woody aerial stems, but *M. rollinsii,* described below, is unusual in the genus in being a shrublet with woody stems and well-developed cork.

It gives us great pleasure to name the new species in honor of Professor Reed C. Rollins, former director of the Gray Herbarium of Harvard University, in recognition of his outstanding revision of *Menonvillea* (Rollins, 1955), in which he described nine new species and proposed new combinations for 12 others.

Menonvillea rollinsii Al-Shehbaz & Marticorena, sp. nov. FIGURE 1.

Fruticulus 15–20 cm altus, ad basin 4–6 mm in diametro; folia succulenta, lineari-subulata, scabra, 4–10 mm longa, 0.8–1.2 mm lata; sepala oblonga, scabra, 2–2.3 mm longa; petala oblonga, alba, 2–2.5 mm longa, marginibus crispis; pedicelli fructiferi recti, divaricati, 4–5 mm longi; fructus glaber, val-

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Journal of the Arnold Arboretum **71**: 135–138. January, 1990.

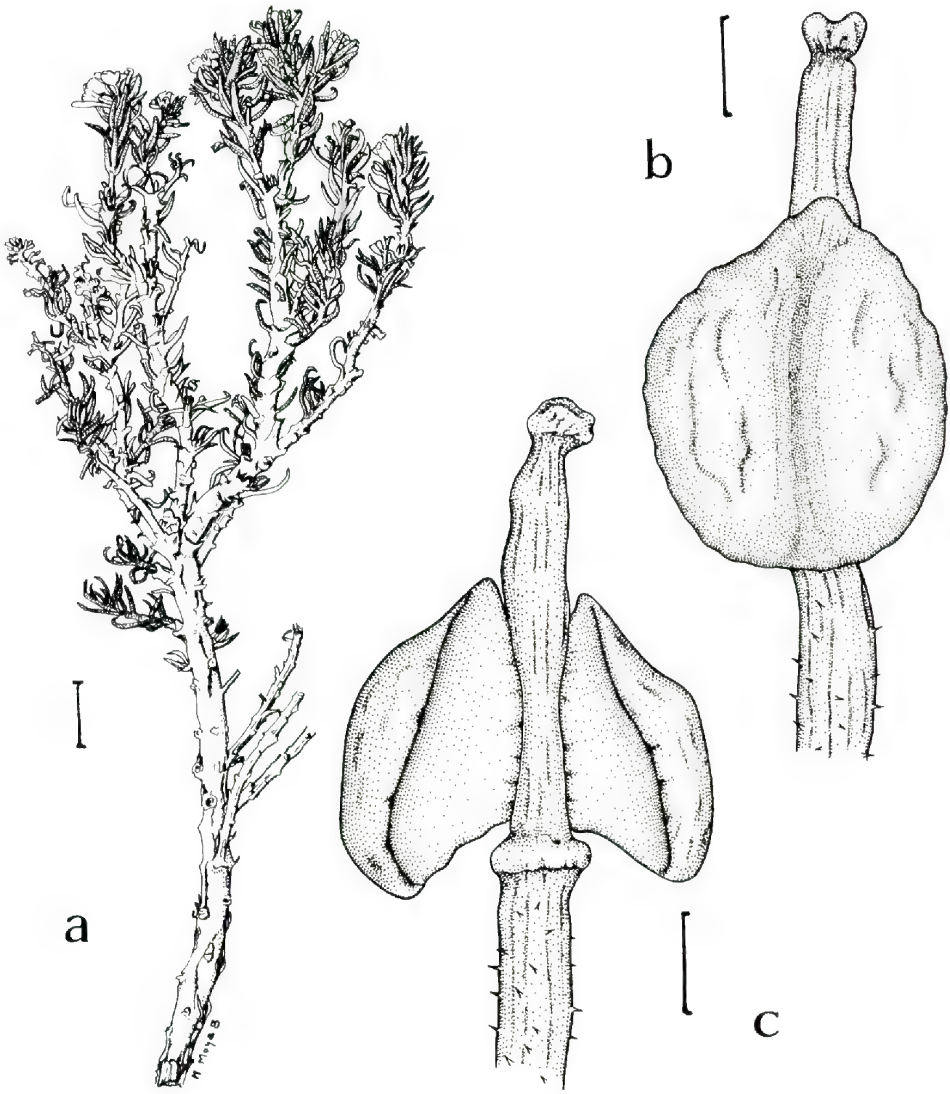

FIGURE 1. *Menonvillea rollinsii* (holotype): a, plant; b, fruit, front view; c, fruit, lateral view. Scale bars = 1 cm (a), 1 mm (b, c).

vibus late ovatibus et anguste alatibus, 2–3 mm longus; stylus 1–1.5 mm longus; semina ignota.

Shrublet 15–20 cm high; sparsely and minutely scabrous almost throughout with trichomes 0.05–0.1 mm long. Old stems straw colored, 4–6 mm in diameter at base. Leaves sessile, fleshy, subulate-linear, scabrous, 4–10 mm long, 0.8–1.2 mm wide, entire, straight or incurved. Inflorescences terminal, few-flowered, ebracteate racemes. Sepals caducous, oblong, 2–2.3 mm long, ca. 1 mm wide, scabrous, scarious at margin. Petals white, oblong, 2–2.5 mm long,

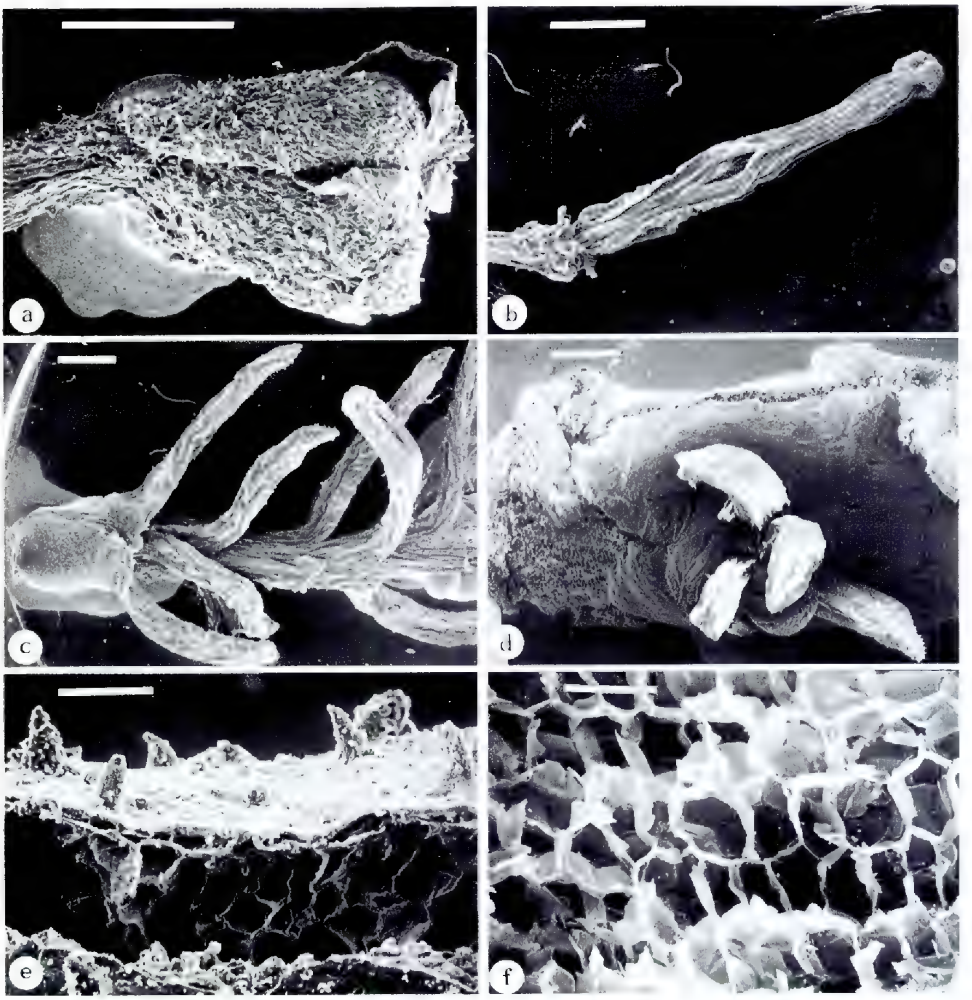

FIGURE 2. Scanning electron micrographs of *Menonvillea rollinsii*: a, flower bud; b, replum; c, leafy branch; d, portion of old stem; e, closeup of crack on old stem, showing trichomes, epidermis, and cork; f, cork. Scale bars = 1 mm (a–d), 0.1 mm (e, f).

ca. 0.8 mm wide, not clawed, uniform in width throughout, crisped at margin. Stamens 6, slightly tetradynamous; filaments erect, ca. 1.8 mm long; anthers oblong, 1–1.1 mm long. Median nectar glands solitary, toothlike; lateral glands ringlike. Fruiting pedicels straight, divaricate, 4–5 mm long. Fruits glabrous, narrowly 4-winged; valves broadly ovate, 2–3 mm long, 1.2–2.2 mm wide, inconspicuously veined on the back, triangular in cross section, each with narrow marginal wing 0.15–0.3 mm wide; style thick, 1–1.5 mm long; stigma capitate, 2-lobed. Seeds not seen.

TYPE. Chile, Región II [Antofagasta], camino de Chuquicamata a Conchi, 2700 m alt., 5 April 1961, *Ricardi, Marticorena, & Matthei 445* (holotype, CONC; fragment, GH).

Menonvillea rollinsii is unique in the genus because of its shrubby habit and its older stems with well-developed cork (see FIGURE 2e, f). It is also easily distinguished from the other species of *Menonvillea* in having short (4–10 mm), sessile, subulate-linear leaves (see FIGURE 2c) and in being scabrous almost throughout (the petals, stamens, and fruits are glabrous) with minute, persistent trichomes only 0.05 to 0.1 mm long (see FIGURE 2e). The species is isolated in the genus and has no known close relatives.

Menonvillea rollinsii grows in open, very dry habitats that have an average annual rainfall of only ca. 9 mm. It is associated with plants such as *Adesmia atacamensis* Philippi, *Argylia tomentosa* Philippi, *Cristaria* Cav. (two species), *Cryptantha linearis* (Colla) Greene, *C. parviflora* (Philippi) Reiche, *Philippiamra pachyphylla* Philippi, *P. fastigiata* Philippi, *Solanum sitiens* I. M. Johnston, *Tetragonia trigona* Philippi, and *Trichocline caulescens* Philippi.

The shrubby habit in the Brassicaceae has evolved independently many times, as is evidenced by its occurrence in unrelated genera of various tribes (Al-Shehbaz, 1984). Apparently, woodiness also evolved independently in *Menonvillea* and in its nearest relative, *Cremolobus* DC., an Andean genus of seven species, of which four are woody and three are herbaceous annuals (Khanna & Rollins, 1965).

ACKNOWLEDGMENTS

We are most grateful to Donald H. Pfister for obtaining funds from the Harvard University Herbaria that supported the SEM portion of this research. We are thankful to Elizabeth A. Shaw for checking the Latin diagnosis, to Neil A. Harriman for his critical review of the manuscript, to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice, to Trisha Rice for the SEM work, to Barbara Nimblett for typing the manuscript, and to N. Moya B. for the illustration.

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BOOK REVIEW

Histoire du Concept d'Espèce dans les Sciences de la Vie, by Scott Atran *et al.* Fondation Singer-Polignac, Paris, 1987. xiii + 324 pp. ISBN 2-900927-19-6. 150 francs softcover.

This valuable book contains 15 chapters based on papers presented at a meeting in May, 1985, held in Paris under the auspices of the Fondation Singer-Polignac. This foundation is named after the Princesse Edmond de Polignac, née Winaretta-Eugénie Singer, who was born in New York in 1865. It is thus appropriate that some papers are in English and others are in French.

The importance of this set of papers is in part, as M. J. S. Hodge notes in his article ("Darwin, Species and the Theory of Natural Selection"), because the contributors have collectively engaged in a study of the *longue durée*—applied to the history of science, the long-term intellectual and institutional life of science. In the past we have tended to consider species concepts in the context of taxonomic species. In this volume many contributors take a refreshingly broad approach to their subject, stepping back from the issues of taxonomic species and species concepts and illuminating issues that are very much current; discussion among biologists is also becoming less introspective. Hodge himself emphasizes ambiguities between conceptualizations of species presupposed by an explanatory program and the definition of species as a classificatory category and shows how Darwin's species concept ultimately depends on the former. From late 1837 to late 1838, Darwin emphasized that cessation of interbreeding was necessary for the adaptation and formation of "good species." However, as the analogy between artificial and natural selection assumed more prominence in his mind, he dropped this requirement, and with it the idea that species occupied a particular rank in the hierarchy of nature. Species as taxa existed, and Darwin recommended following the species limits of the masters of the art, but there were no criteria other than custom for ranking species.

Phillip Sloan ("From Logical Universals to Historical Individuals: Buffon's Idea of Biological Species") takes a similar approach. He shows how Buffon integrated contemporary discussion on issues such as calculus and probability with William Harvey's separation of two senses in which species were used in the work of Aristotle. Buffon distinguished between mathematical truth, which was arbitrary and abstract, and physical truth, which was grounded in fact and had a probability approaching certainty. Hence Buffon rejected species as universals—they were abstract—and accepted species as wholes and individuals, rather than as collections of things. To Buffon, it was not the individual in the strict sense, but the chain of successive individuals that constituted the species, that was the great marvel. Genealogy, but not only of species, was all; classi-

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fication was to be true "Naturgeschichte," not just "Naturbeschreibung." However, as Sloan has discussed elsewhere, the latter predominated. The reasons for this need detailed study. A contributing factor may be that the only tool by which genealogy could be directly established remained for almost two hundred years the ability to interbreed. This surely meant that Buffon's ideas at the species level could be difficult to distinguish from more conventional species concepts. Yet in many of these, even the most "fixist," genealogy and individuality of a sort were very important; it is only now that details of the relationship between morphology and genealogy are being teased apart.

Richard Burkhardt, Jr. ("Lamarck and Species") suggests that Lamarck did not alter the way in which he described taxonomic species, despite his changing ideas about what species represented in the natural world. Taxonomy even then had its own requirements (which it has been inclined to defend against the natural world ever since!). Toward the end of Lamarck's life, it seems that his concept of species reverted from nominalist back to the position that he held when writing the *Flore Françoise*—that they were real. Unfortunately, Burkhardt's discussion does not allow us to establish clearly enough the context of the change. Intergradation, for Lamarck, was a geographic as well as a temporal phenomenon, but at any one time and place species would be discrete.

The issue of what such locally discrete species represent figures largely in Scott Atran's paper ("The Early History of the Species Concept: an Anthropological Reading"). He observes that taxa in the fundamental rank of folk classification, the generic-specieme (in the strict sense, the representative of a genus growing in a local area), were recognized using morpho-ecological criteria; unlike some authors, Atran dismisses more culturally bound concerns, such as utility, as having little effect. Breeding criteria were introduced into species concepts by Andrea Cesalpino and John Ray as knowledge developed a broader geographic base: organisms that bred true showed only accidental variation and formed the abstract types that could be placed in a universal taxonomy.

There are still major tensions between the folk species concept (or, more properly, the generic-specieme concept), the nondimensional species that Ernst Mayr ("The Species as Category, Taxon and Population") defends vigorously, and the taxonomic species. Mayr emphasizes the interest of biologists in sympatric situations and local populations, the potential status of an allopatric population being usually biologically rather uninteresting for Mayr. Some of these tensions have obvious causes, as in Mayr's article: for instance, the term "population" is not clearly defined and the taxonomic-morphological species is equated with the typological (Donn Rosen's species are branded as "typologically defined morphospecies").

For Bernardino Fantini ("L'Entrée de la Biologie Moléculaire dans la Définition de l'Espèce") the definition of species as a taxonomic unity remained untouched by molecular biology, which has focused on mechanisms of speciation. Untouched or passed by? The biological species concept was championed by Mayr in 1942 so that the origin of species could be discussed. But for this, species either have to be the units that evolved, or to stand in some static relationship to those that did (Mayr discusses stasis briefly). Birds (perhaps) aside, are taxonomic species in general units of this sort? Can they be,

should they be, and what are the consequences for both taxonomy and biology of the various ways in which these questions are answered?

Anne Diara introduces such questions in her paper, appropriately titled "Les Espèces Sont-Elles Filles de la Nature ou du Naturaliste?" She discusses the apparent conflict between the species concepts of Alexis Jordan, a misanthropic royalist and fixist who circumscribed species very closely, and Charles Naudin, a much more central figure on the French biological scene who came to believe in evolution by 1852 (but never seems to have accepted natural selection). Diara suggests rightly that the argument was less over "facts" than how those "facts" should be interpreted (see also Jean-Louis Fischer, "Espèce et Hybrides: à Propos des Léporides"). As she notes, the taxonomic philosophy of Jordan (of whom Naudin contemptuously remarked that, with all his new species, he had not introduced a single new fact into science) was agreeable to Hugo de Vries. De Vries's work, reinterpreted although it soon was, nevertheless focused attention on the nature of the Linnaean species. Diara briefly discusses a series of papers on species concepts in the *American Naturalist* of 1908, and she sees Linnaean classification as being maintained primarily for logical reasons. Further development of this point would have brought the arguments closer to home (and would probably have made the article far too long). Linnaean species, at least in the context of the polemics of that time, were broadly circumscribed, yet despite all the lip service paid to them, few of the botanists who extolled their virtues over the next fifty years—a list would be surprising in both length and content—were able to find biological reasons for maintaining them.

One is left feeling that what one thinks might matter when it comes to the delimitation of species, does not, and what should not, does. The requirement that taxonomic species be readily recognizable is clearly responsible for much of this confusion. Mary P. Winsor (Louis Agassiz and the Species Question, Studies Hist. Biol. **3:** 89–117. 1979) shows how hard it is to provide a reasonable evaluation of the link between species concepts and species taxa; overall, it was not Agassiz's ideas that were unscientific but his dogmatism. It was not simply because Jordan did not believe in evolution that he described so many new species from France; splitters are not necessarily "typologists." His fixist colleagues did not rise to his defense, while others found it hard to dismiss all his species as being absolutely worthless due to the very fact of evolution.

Evolution has only gradually shaped species concepts and species taxa. In ornithology this change was greatly helped by the new "nomenclatural" code proposed by the American Ornithologists' Union in 1885. Antonello La Vergata ("Au Nom de l'Espèce. Classification et Nomenclature au XIXe Siècle") shows that apparently arid nomenclatural debates over the name of a species may be, as he puts it, carried out in the name of the species, that is, a particular conception of nature. How authorities were cited when a species was transferred from one genus to another depended quite largely on whether species were conceived of as logically (and biologically) part of the genus in which they were placed (the Linnaean position), or the species (both as rank and taxon) was seen as more real than the genus. Priority does not necessarily have to do with the rights of the dead, but rather with the concepts of the living. Another

nomenclatural dispute that involves similar issues and that would repay study concerns species groups. These were ultimately accepted in zoology, in part because they were seen to be compatible with evolution, and rejected in botany.

Returning to a theme of the book, discussions about species concepts must often range beyond taxonomy if they are to be properly understood: arguments about nomenclature and classification may be so bitter and protracted precisely because there are larger issues at stake. Furthermore, there are only partly overlapping groups of people using terms such as "species." Pietro Corsi ("Julien Joseph Virey, le Premier Critique de Lamarck") shows how Virey's writings, with their implicit and explicit species concepts, reached a wide segment of the francophone world (as is also true of Buffon's work). What does today's public think is being saved when a species is conserved, and where did they get their ideas?

There are other useful essays; here I have focused on those most of interest to botanists. Although it may be a little hard to get hold of a copy of this book, it is most highly recommended for all biological libraries, and it is even not out of reach of less-than-well-paid taxonomists. The issues raised in it demand serious thought. The editing is on the whole good, although I think that three spellings for "armadillo" in eight lines must be something of a record; Qaddafi will have to look to his laurels in this department.—P. F. STEVENS, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

XV International Botanical Congress, Tokyo

The Organizing Committee of the XV International Botanical Congress wishes to announce that the XV IBC will be held in the Tokyo area during August and September 1993: the nomenclature session 23–27 August, and the general session 28 August–3 September. The first circular for the XV IBC will be prepared in 1990 and will be distributed to those who are interested in the Congress. Requests for information and other questions and comments may be sent to:

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Bunkyo-ku, Tokyo 113
Japan

U.S. Postal Service

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Required by 39 U.S.C. 3685)

1A. Title of Publication	1B. PUBLICATION NO	2. Date of Filing
JOURNAL OF ARNOLD ARBORETUM	0 0 0 4 2 6 2 5	Sept 15, 1989
3. Frequency of Issue	3A. No. of Issues Published Annually	3B. Annual Subscription Price
Quarterly	4	$70.00

4. Complete Mailing Address of Known Office of Publication *(Street, City, County, State and ZIP+4 Code) (Not printer)*

1041 New Hampshire St. Lawrence, Ks. 66044

5. Complete Mailing Address of the Headquarters of General Business Offices of the Publisher *(Not printer)*

Same as #4

6. Full Names and Complete Mailing Address of Publisher, Editor and Managing Editor *(This item MUST NOT be blank)*

Publisher *(Name and Complete Mailing Address)*

Arnold Arboretum of Harvard University, 1041 New Hampshire St. Lawrence, Ks. 66044

Editor *(Name and Complete Mailing Address)*

S.A. Spongberg 22 Divinity Ave. Cambridge MA 02138

Managing Editor *(Name and Complete Mailing Address)*

E.B. Schmidt 22 Divinity Ave. Cambridge MA 02138

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Full Name	Complete Mailing Address
Arnold Arboretum of Harvard University	1041 New Hampshire ST. Lawrence, KS 66044

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9. For Completion by Nonprofit Organizations Authorized To Mail at Special Rates *(DMM Section 423.12 only)*
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10. Extent and Nature of Circulation *(See instructions on reverse side)*	Average No. Copies Each Issue During Preceding 12 Months	Actual No. Copies of Single Issue Published Nearest to Filing Date
A. Total No. Copies *(Net Press Run)*	750	750
B. Paid and/or Requested Circulation 1. Sales through dealers and carriers, street vendors and counter sales		
2. Mail Subscription *(Paid and/or requested)*	527	558
C. Total Paid and/or Requested Circulation *(Sum of 10B1 and 10B2)*	527	558
D. Free Distribution by Mail, Carrier or Other Means Samples, Complimentary, and Other Free Copies	12	12
E. Total Distribution *(Sum of C and D)*	539	570
F. Copies Not Distributed 1. Office use, left over, unaccounted, spoiled after printing	211	180
2. Return from News Agents		
G. TOTAL *(Sum of F, F1 and 2—should equal net press run shown in A)*	750	750

11. I certify that the statements made by me above are correct and complete

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PS Form **3526**, Feb. 1989 *(See instructions on reverse)*

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Volume 70, Number 4, including pages 443–541, was issued 11 October 1989.

JOURNAL OF THE ARNOLD ARBORETUM

HARVARD UNIVERSITY VOLUME 71 NUMBER 2

ISSN 0004–2625

Journal of the Arnold Arboretum

The *Journal of the Arnold Arboretum* (ISSN 0004-2625) is published quarterly in January, April, July, and October for $70.00 per year, plus $10.00 or $15.00 postage for addresses outside of the United States, by the Arnold Arboretum of Harvard University. It is printed and distributed by Allen Press, Inc., 1041 New Hampshire Street, Lawrence, Kansas 66044. Second-class postage paid at Lawrence, Kansas. POSTMASTER: send address changes to *Journal of the Arnold Arboretum*, % Allen Press, Inc., P.O. Box 368, Lawrence, Kansas 66044.

Because publication of the *Journal of the Arnold Arboretum* is being suspended after Volume 71 (1990) has been completed, subscriptions can only be accepted for the present volume. Remittances for Volume 71 should be sent to *Journal of the Arnold Arboretum*, 1041 New Hampshire Street, Lawrence, Kansas 66044, U.S.A. Claims will not be accepted after six months from the date of issue.

Volumes 1–51, reprinted, and some back numbers of volumes 52–56 are available from the Kraus Reprint Corporation, Route 100, Millwood, New York 10546, U.S.A.

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Printed at Allen Press, Inc., Lawrence, Kansas

COVER: The stylized design appearing on the Journal and the offprints was drawn by Karen Stoutsenberger.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 71 APRIL 1990 NUMBER 2

THE GENERA OF ARUNDINOIDEAE (GRAMINEAE) IN THE SOUTHEASTERN UNITED STATES[1, 2]

GORDON C. TUCKER[3]

Subfamily ARUNDINOIDEAE Tateoka, Jour. Jap. Bot. **32:** 277. 1957, "Arundoideae."

Perennial or annual, small to very large herbaceous plants of wetlands, woodlands, and lowland and montane grasslands [semideserts]. Rhizomes often present. Stems erect or spreading (stolons sometimes present); nodes solid,

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8716834 (Norton G. Miller, principal investigator), under which this account was prepared, and BSR-8717333 (Carroll E. Wood, Jr., principal investigator). This treatment, 132nd in the series, follows the format established in the first paper (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. Those references I did not verify are marked with asterisks.

I have continued to enjoy working with Norton Miller and Carroll Wood on the Generic Flora project and I thank them for their interest and advice. William J. Crins, Ihsan A. Al-Shehbaz, and Barbara Nimblett have helped frequently. Mary E. Barkworth (Utah State University) and Stephen J. Darbyshire (Agriculture Canada, Ottawa) reviewed the manuscript and made numerous valuable suggestions. Elizabeth B. Schmidt and Stephen A. Spongberg improved the final manuscript with their editorial skills. Thanks are extended to the staffs of the New York State Library (especially Alta Beach, Senior Librarian) and the Botany Libraries of Harvard University (especially Geraldine C. Kaye, Librarian) for providing many references. I thank the curators of the following herbaria who have sent specimens or provided access to collections and hospitality during my visits: A, ALU, CCNL, CONN, DUKE, ECON, GH, NEBC, NYS, TRT, UNA, US.

Contribution number 625 of the New York State Science Service.

[2]The illustrations (by Karen Stoutsenberger from dissections by Carroll Wood) are rearrangements of parts of FIGURES 3, 5, and 7 in C. S. Campbell's account of the family Gramineae, its subfamilies, and tribes in the southeastern United States (Jour. Arnold Arb. **66:** 123–199. 1985).

[3]Biological Survey, New York State Museum, Albany, New York 12230.

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glabrous, pubescent, or puberulent. Leaves several, basal and cauline, or cauline only; sheath margin open; blade linear to narrowly lanceolate; bundle sheaths double; chlorenchyma not radiate (except in *Aristida* and *Neyraudia*); silica bodies of various shapes, longitudinally oriented; stomata not dominating intercostal zones, subsidiary cells domed. Inflorescences terminal or terminal and axillary (axillary cleistogamous ones wholly enclosed within sheaths in *Danthonia* and *Nassella*). Spikelets few to very numerous, laterally flattened to subcylindrical, 1- to several-flowered; articulation above the glumes. Glumes 2, subequal to decidedly unequal, lanceolate, equaling or shorter than the lemmas; lemmas conduplicate, involute, or convolute, membranaceous (or indurate). Paleas shorter and narrower than the lemmas. Lodicules [3] 2 (or lacking), oblong or obtruncate, entire or shallowly emarginate, the margin sometimes ciliate. Stamens 1 or 3; filaments slender; anthers ellipsoid to linear. Ovaries ellipsoid to cylindrical. Fruit a caryopsis [achene], cylindrical or flattened, more or less clasped by persistent lemma and palea. Pericarp adnate to [free from] the seed. Hilum ovate-oblong to linear. Base chromosome numbers 9, 10, 11, 12. (Including Aristideae C. E. Hubb., Centothecoideae Soderstrom, Danthonieae Zotov, Stipeae Dumort.) TYPE GENUS: *Arundo* L.

A subfamily of about 60 genera and some 1400 species, in five tribes, distributed worldwide but with the greatest diversity, both in species and genera, in the Temperate Zone of the Southern Hemisphere. The Arundinoideae are represented in the Southeast by seven genera in four tribes (Aristideae C. E. Hubb., Arundineae Dumort., Centotheceae Ridley, Stipeae Dumort.) and a total of 43 species, half of them in *Aristida* L.

The circumscription of the subfamily has undergone numerous modifications and is accepted here in the sense of Campbell and Davidse and colleagues to include the Centotheceae, and in the sense of Barkworth & Everett to include the Stipeae, which were treated as an unplaced tribe by Campbell. Narrower circumscriptions have been proposed by Clayton & Renvoize, Conert (1987), and Renvoize (1982).

In an extensive cluster analysis using 71 characters, Renvoize (1982) demonstrated the importance of leaf-blade anatomy in defining a core group of genera. Several genera, such as *Neyraudia* Hooker f., combine features of the Arundinoideae with those of other traditional subfamilies. In a phylogenetic analysis of the family, Kellogg & Campbell concluded that the subfamily is polyphyletic and probably consists of several groups that are basal to other major clades (i.e., subfamilies) of the grasses.

Danthonia DC. and its allies were included in the Aveneae Dumort. (Pooideae) by Bentham (1883) and Hitchcock (1951) because of their glumes about as long as the spikelets, their several florets per spikelet, and their twisted geniculate lemma awns. Various studies (summarized by Campbell) have pointed out differences between the avenoids and the danthonioids in cytology, leaf anatomy, and embryology. The danthonioids were first accorded tribal status by Zotov, and their similarity to the arundinoids has since been further demonstrated by Hilu & Wright (1982) and Renvoize (1982).

The reed grasses, *Gynerium* Beauv., *Phragmites* Adanson, and *Thysanolaena*

Nees, have chlorenchyma cells with invaginated walls, a bambusoid feature. *Neyraudia* has radiate chlorenchyma (possibly C_4) and is similar and transitional to the Chloridoideae. However, it lacks other chloridoid features such as egg-shaped microhairs, cruciform silica bodies, and triangular subsidiary cells. It has slender arundinoid microhairs, but its embryo is eragrostoid. Its resemblance to *Arundo* and *Phragmites* seems to be due to convergent evolution of habit, not taxonomic affinity (Clayton & Renvoize). The presence of kranz anatomy suggests that species of *Neyraudia* are C_4, but biochemical and isotopic studies have not yet been conducted to confirm this.

Cortaderia Stapf is a danthonioid genus of about 24 species, with greatest diversity in the Andean and Pampan regions of South America. There are also four species in New Zealand and one in New Guinea. *Cortaderia Selloana* (Schultes) Ascherson & Graebner, pampas grass, is cultivated as an ornamental in warm regions of the United States. Evidence that it spreads from cultivation is lacking, although plants persisting after cultivation have been reported from North Carolina (Radford *et al.*) and Texas (Gould). In California, it is a non-spreading and popular cultivated species. Another cultivated species, *C. jubata* (Lem.) Stapf ("C. atacamensis"), a South American native, is an invasive weed along the California coast (Cowan). In California, only carpellate plants are known and abundant seed is produced apomictically (Costas Lippmann, 1977). It is also a bad weed in New Zealand (Knowles & Ecroyd).

Another danthonioid genus, *Schismus* Beauv., is represented in the southwestern United States and adjacent Mexico by two Eurasian adventives, *S. barbatus* (L.) Thell. (Gould & Moran) and *S. arabicus* Nees.

The Aristideae, the only largely C_4 tribe of the Arundinoideae, include just three genera: *Aristida, Sartidia* De Winter, and *Stipagrostis* Nees. It is distinctive both in spikelet morphology and leaf-blade anatomy (Renvoize, 1986). Anatomically, the inner layer of cells in the two-layered bundle sheaths is as large as or larger than the outer layer. The three genera can also be distinguished anatomically. In *Sartidia* the chlorenchyma is not radiate and the photosynthetic pathway is C_3. *Stipagrostis* (sometimes included in *Aristida*) and *Aristida* are both C_4 genera. In *Stipagrostis* there are no chloroplasts in the inner layer, while in *Aristida* they are present.

The unigeneric tribe Micraireae Pilger is endemic to northern Australia (Clayton & Renvoize; Lazarides). There are 13 species of *Micraira* F. Mueller, all of which grow in very thin soil and show an adaptation to this habitat condition in their ability to recover from extreme desiccation. The genus is unique in the family in having spiral phyllotaxy. The base chromosome number is 10.

The monotypic tribe Thysanolaeneae C. E. Hubb. includes only *Thysanolaena maxima* (Roxb.) O. Kuntze, $2n = 24$, of tropical southern and southeastern Asia. The genus is related to *Phragmites* and may not warrant tribal status (Clayton & Renvoize).

The Centotheceae are a small group of 11 genera and 26 species (ca. 30, *fide* Clayton & Renvoize; Tenório). Except for *Chasmanthium* Link, which is endemic to southeastern North America, and *Gouldochloa* Valdés, Morden, & Hatch, endemic to northeastern Mexico, they are pantropic. Centothecoids are similar to the herbaceous bambusoids in habit but are decidedly arundinoid

in leaf anatomy. The distinctive embryos have a mesocotyl, lack an epiblast (present in other arundinoids), and have a scutellum cleft and a rolled first leaf. Centothecoid grasses were first accorded taxonomic notice as a subtribe of the Festuceae (= Poeae) by Bentham (1883). They were subsequently treated as subfam. Centothecoideae (Clayton & Renvoize; Soderstrom; Tenório) but are here considered to be a tribe of the Arundinoideae following Campbell and Davidse and colleagues. A strongly papillate abaxial surface (absent in other grasses) characterizes all genera (Davidse *et al.*). The spikelets are strongly laterally compressed, the caryopsis is laterally flattened, and the hilum is basal and punctiform to shortly linear. Many genera have pulvinate petiolate leaves (*Chasmanthium* and *Gouldochloa* are exceptions), double bundle sheaths, and leaf tissue differentiated into palisade and spongy layers (in grasses otherwise known only in *Laciasis* (Griseb.) Hitchc., Panicoideae A. Br.). Bicellular, often filiform microhairs are commonly present (Davidse *et al.*). A base chromosome number of 12 characterizes nearly all cytologically known genera.

The only large genus, *Zeugites* R. Br., is confined to the New World tropics, as are *Calderonella* Soderstrom & Decker and *Pohlidium* Davidse, Soderstrom, & Ellis. In the Old World tropics are *Bromuniola* Stapf & Hubb., *Centotheca* Desv., *Chevalierella* A. Camus, *Lophatherum* Brongn., and the most primitive genus, *Megastachya* Beauv. Only *Orthoclada* Beauv. has representatives in both the Old World and the New. Tenório proposed (but did not validly publish) a monotypic genus for the African species of *Orthoclada*.

The Stipeae are here included in the Arundinoideae, as has been suggested by Barkworth & Everett and Watson and colleagues. However, Kellogg & Campbell hypothesized that the Stipeae form a clade that is the sister group of the Pooideae. Their amino-acid profiles are intermediate between those of the pooids and the bambusoids. Two-celled microhairs are absent from the Stipeae, as they are from the Pooideae. However, single-celled microhairs, called "pylidial hairs" by Renvoize (1985), are present in some species of *Stipa* and *Oryzopsis* sensu lato. These hairs may have evolved from the two-celled, fingerlike microhairs of Bambusoideae. In the Southeast the Stipeae are represented by two genera, *Nassella* (Trin.) Desv. and *Piptochaetium* J. Presl, each of which has been included in *Stipa* by some workers.

The stipoid genus *Oryzopsis* Michx. (including *Piptatherum* Beauv.) is represented by ten or more species in North America, mostly in the West. Three species, *O. asperifolia* Michx., *O. canadensis* (Poiret) Torrey, and *O. racemosa* (J. E. Sm.) Ricker, reach their southern range limits in the mountains of West Virginia and may yet be found in the mountains of North Carolina and Tennessee. The western species *O. hymenoides* (Roemer & Schultes) Ricker, $2n = 48$, comes eastward to Manitoba, Kansas, and western Texas and might be expected as an adventive or waif in Arkansas or Louisiana.

Although the genus *Milium* L. was included in the Stipeae by Clayton & Renvoize, who made the amazing statement that it is merely an awnless version of *Oryzopsis*, it was excluded from the tribe by Barkworth & Everett. According to anatomical data provided by Renvoize (1985), *Milium* is anomalous in the Stipeae in having tapering long cells and in lacking short cells in the leaf epidermis. It is typically pooid in its leaf anatomy, amino-acid profile, susceptibility to rusts, and cytology (see Barkworth & Everett for references).

Haustorial synergids, an unusual micromorphological feature not otherwise known in the grasses, have been found in *Chionochloa* Zotov, *Cortaderia, Danthonia* (including *Rytidosperma* Steudel), *Erythranthera* Zotov, *Lamprothyrsus* Pilger, *Pyrrhanthera* Zotov, and *Sieglingia* Bernh. (Philipson & Connor). These massive synergids extend through the micropyle to lie between the ovule and the ovary wall. Normal pyriform synergids, the typical graminoid condition, characterize *Arundo* and *Phragmites.* The ovary in *A. Donax* L. has an unusually long stalk (Bhanwra). The outer epidermal cells of the ovary accumulate an unidentified darkly staining material in *A. Donax* and *P. Karka* (Retz.) Trin. ex Steudel (Bhanwra). Intercalary growth of the chalaza after fertilization characterizes all arundinoid grasses investigated.

Information on the reproductive biology of the arundinoid grasses is incomplete. Most genera have perfect flowers. Species of *Cortaderia* and *Lamprothyrsus* are gynodioecious. The Neotropical *Gynerium sagittatum* (Aublet) Beauv., the only species of the genus, is dioecious. Self-compatibility is known in some species of *Aristida, Chasmanthium, Chionochloa, Cortaderia, Danthonia* (including some species assigned to the segregate *Rytidosperma*), *Nassella,* and *Stipa. Phragmites australis* is apparently self-incompatible. Apomixis is reported from *Cortaderia jubata* (Philipson, 1978). Four genera in our area (*Aristida, Chasmanthium, Danthonia,* and *Nassella*) produce cleistogamous as well as chasmogamous spikelets in at least one species. In most genera (all those in the Southeast) the pericarp is fused to the seed coat (ordinary grass caryopsis). However, in several (none in the Southeast) the pericarp is free or separable and the fruit is thus an achene. The genera with achenes are *Amphipogon* R. Br. (Australia), *Anisopogon* R. Br. (Australia), *Dregeochloa* Conert (southern Africa), *Elytrophorus* Beauv. (tropical Africa, India, Australia), *Hakonechloa* Honda (Japan), *Pentameris* Beauv. (southern Africa), *Pyrrhanthera* (New Zealand), and *Urochlaena* Nees (southern Africa). With "reluctantly free pericarp" (Clayton & Renvoize, p. 182) are *Molinia* Schrank (temperate Eurasia) and *Tribolium* Desv. (southern Africa). Except for *Hakonechloa,* all the genera with a free pericarp are confined to the Southern Hemisphere (or to continents derived from Gondwanaland).

The dispersal mechanisms of most arundinoid grasses depend on hairs or awns. The mature spikelets of *Neyraudia* and *Phragmites* break at the joints of the fragile rachilla. The hairs of the rachilla allow the florets to be wind dispersed. The silky, clasping lemmas of *Arundo* probably serve the same function. The long, sharp awns and short, stiff callus hairs of the lemmas of *Aristida* species cause the mature spikelets to stick in fur or skin of animals and thus to be dispersed. Peart, however, examined carcasses of some 100 marsupials and found no awned diaspores in their fur, a surprising result in Australia, where both *Aristida* and *Danthonia* are diverse. African species of *Stipagrostis* have plumose awns, enabling dispersal by wind. The awns of the lemmas of *Danthonia* species are hygroscopic, twisting and coiling and moving the floret into soil crevices, where chances for its germination are improved (Peart). (The hygroscopic awn of *Piptochaetium* may function in the same way.) The long hairs of the lemmas of the Australian *D. tenuior* (Steudel) Conert collapse on drying and rehydrate on wetting, moving the diaspores across soil and into crevices (Peart).

The arundinoid grasses are little known chemically. The leaves of *Phragmites australis* contain flavonoid aglycones (chrysoeriol, isorhamnetin, luteolin, quercetin, tricin), flavonol and flavone *O*-glycosides (e.g., glucosyl-3 quercetin and glucosyl-7 tricin), and flavone *C*-glycosides (7,3′-dimethoxy-isoorientin, isoorientin, isoscoparin, swertiajaponin, swertisin). Tricin and *C*-glycoflavones are known from about 90 percent of the grasses that have been studied (Jay & Viricel). The major flavonoid components of the "flower tissue" (= spikelets?) of *P. australis* are isoswertiajaponin and swertiajaponin (Nawwar *et al.*); also noted were 3′*O*-gentiobioside and the 3′-*O*-glucoside of swertiajaponin. In addition, there are two flavonol glycosides, rhamnetin 3-*O*-rutinoside and rhamnetin 3-*O*-glucoside, a class of compounds rare in grasses. *Phragmites australis* has a minute (0.27 percent) hydrocarbon fraction and no appreciable polyisoprenes (Buchanan *et al.*). The epicuticular layer of *Chionochloa* species contains long-chain carbon compounds (alcohols, aldehydes, alkanes, esters, and fatty acids) up to 52 carbons in length (Savill *et al.*).

Numerous fungi parasitize arundinoid grasses. *Balansia hypoxylon* (Peck) Atk. (anamorph: *Ephelis borealis* Ellis & Everhart) parasitizes *Danthonia compressa* Austin, *D. sericea* Nutt., and *D. spicata* (L.) Beauv., as well as *Aristida glauca* (Nees) Walp. and three species of *Stipa*. It forms segmented sclerotia (Sprague). *Uromyces Danthoniae* McAlp. occurs on six Australian species of *Danthonia*; however, no rusts are reported from any New World species of *Danthonia*. *Puccinia invenusta* H. Sydow & P. Sydow grows on all three species of *Phragmites* in the Old World but has no other hosts. *Puccinia Magnusiana* Körn. (worldwide) and *P. Trabutii* Roum. & Sacc. (northern Africa, southern Asia) both occur on *Arundo* and *Phragmites*. *Puccinia Neyraudiae* H. Sydow & P. Sydow is reported only from *Neyraudia madagascariensis* (Kunth) Hooker f. in southern India (Cummins).

The earliest evidence of arundinoid grasses dates from the Miocene. In a fine study Thomasson (1984) demonstrated anatomical features in silicified remains from Nebraska. Fossilized florets of the extinct stipoid genus *Berriochloa* M. K. Elias were found in the abdominal cavity of a fossilized rhinoceros, *Teleoceras major* Hatcher, and provide direct evidence of grass diet in Miocene times (Voorhies & Thomasson). Quaternary remains of *Phragmites australis* from Egypt could be confidently identified because the internal and external structures of rhizomes and attached stem bases were preserved (El-Saadawi *et al.*).

Plants of the subfamily have some economic importance. None are used for grain. Stems of *Arundo* and *Phragmites* are harvested for paper pulp in Europe and Asia, and they are sometimes important for forage. *Danthonia* species are important for forage in Australia (and to a lesser extent in western North America), as are immature plants of *Aristida* in the American Southwest, but neither is important in these respects in the Southeast. *Nassella leucotricha* is an important cool-weather forage grass in Texas. *Stipa tenacissima* L. is gathered for paper pulp in Algeria and Spain (Hitchcock, 1951).

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Key to the Genera of Arundinoideae in the Southeastern United States

General characters: *perennial or annual herbaceous plants of dry to wet places. Leaf blades linear to lanceolate, flat or involute. Inflorescences paniculate (rarely racemose), terminal and/or axillary. Spikelets laterally compressed or subterete. Glumes 2, conspicuous; flowers 1 to several, disarticulating above glumes; lemmas often awned.*

A. Flowers imperfect or perfect (plants gynodioecious), forming dense tussocks. ..... [*Cortaderia.*]

A. Flowers perfect (lower florets sometimes imperfect); plants rhizomatous, or loosely to densely caespitose.

B. Plants large; leaves cauline only.

C. Rachillas glabrous; lemmas pilose throughout. ..... 1. *Arundo.*

C. Rachillas pilose; lemmas glabrous or pilose on margins only.

D. External ligules a line of hairs; lateral inflorescences often present; lemmas with excurved awn. ..... 3. *Neyraudia.*

D. External ligules absent; inflorescences strictly terminal; lemmas awnless. ..... 2. *Phragmites.*

B. Plants small to medium; leaves basal and cauline.

E. Spikelets subterete, 1-flowered; lemmas indurate, involute.

F. Lemma awns 1-parted.

G. Paleas rudimentary. ..... 6. *Nassella.*

G. Paleas slightly longer than and protruding from apex of lemmas. ..... 7. *Piptochaetium.*

F. Lemma awns 3-parted. ..... 5. *Aristida.*

E. Spikelets laterally flattened, 2- to 12-flowered; lemmas membranaceous, conduplicate.

H. Glumes and spikelets about the same length; lemmas awned; caryopses subcylindrical; leaves mostly basal. ..... 4. *Danthonia.*

H. Glumes much shorter than spikelets; lemmas awnless; caryopses laterally flattened; leaves mostly cauline. ..... 8. *Chasmanthium.*

Tribe ARUNDINEAE Dumortier, Obs. Gram. Belg. 82. 1824.

1. **Arundo** Linnaeus, Sp. Pl. **1:** 81. 1753; Gen. Pl. ed. 5. 35. 1754.

Very large perennials of sunny, damp soils and shallow, fresh waters. Roots fibrous; rhizomes stout. Stems stout, solid, glabrous; nodes glabrous. Leaves several, cauline; sheath glabrous; ligule membranaceous, margin minutely ciliate; blade lanceolate, auriculate, the margin and apex scabridulous; cross veins numerous. Inflorescences single, terminal, much branched, plumose. Spikelets lanceolate; glumes 2, lanceolate, as long as the spikelets; rachilla slender, flattened, glabrous; florets [1 or] 2; lemmas lanceolate, clasping, membranaceous to firm, 5- to 9-nerved, the lower ½ pilose; paleas lanceolate, ½–⅔ as long as the lemmas, hyaline, the margin ciliate. Stamens 3; anthers linear, the apex and base of thecae divergent. Ovaries slenderly cylindrical; styles 2, free, very slender; stigmas slightly longer than styles, plumose, laterally exserted. Caryopses oblong, smooth; hilum short; embryo large. Base chromosome number 12. LECTOTYPE SPECIES: *A. Donax* L.[4] (Name from Latin word for cane.)—GIANT REED.

A genus of three species native to the Old World. *Arundo Donax* L., $2n = 110$, the only wide-ranging species, occurs from Spain to India. The other species are *A. Plinii* Turra, $2n = 72$, of the Mediterranean region, and *A. formosana* Hackel, endemic to Taiwan.

Arundo Donax is naturalized from seed of planted specimens in the southeastern and southwestern United States. I have examined specimens from Virginia, North Carolina, Florida, Louisiana, Texas, and California.

Seed set is reported to be poor in *Arundo Donax* in India because of the failure of meiosis in a majority of the ovules (Bhanwra).

The reeds for woodwind instruments are cut from the stems of *Arundo Donax* (Clayton & Renvoize). The stems are used for thatch in southern Europe, Asia, and Africa, cellulose for paper pulp, and fodder. *Arundo Donax* is also cultivated around pools and on streambanks as an ornamental.

REFERENCES:

Under subfamily references see BAILEY *et al.*; BHANWRA; CLAYTON & RENVOIZE; CONERT (1961); MUNZ; RENVOIZE (1986); TUTIN; and WALTERS *et al.*

2. **Phragmites** Adanson, Fam. Pl. **2:** 34, 559. 1763.

Tall, rhizomatous perennials of swamps, marshes, ditches, and roadsides. Roots fibrous; rhizomes stout, scaly, horizontal to oblique; long stolons often produced by terrestrial plants. Stems glabrous, often glaucous. Leaves cauline, 10–15; sheaths overlapping, with margin free for entire length, glabrous; ligule

[4]Linnaeus included six species in his diverse genus *Arundo*. The genus was typified by removal of five of these: *A. Bambos* L. to *Bambusa* ("Bambus") by Gmelin (Syst. Nat. ed. 13 **2**(1): 579. 1791); *A. Phragmites* L. to *Phragmites* by Adanson (Fam. Pl. 34, 559. 1763); *A. epigejos* L. and *A. Calamagrostis* L. to *Calamagrostis* by Adanson (*Ibid.* 31, 530); and *A. arenaria* L. to *Ammophila* by Host (Gram. Austr. **4**: 24. *pl. 41.* 1809), leaving only *A. Donax*. Linnaeus (Gen. Pl. 35. 1754) described the lemmas as pilose (valvulae . . . basi lanugo") in *Arundo*, a feature fitting only *A. Donax* among the species he included in *Arundo*.

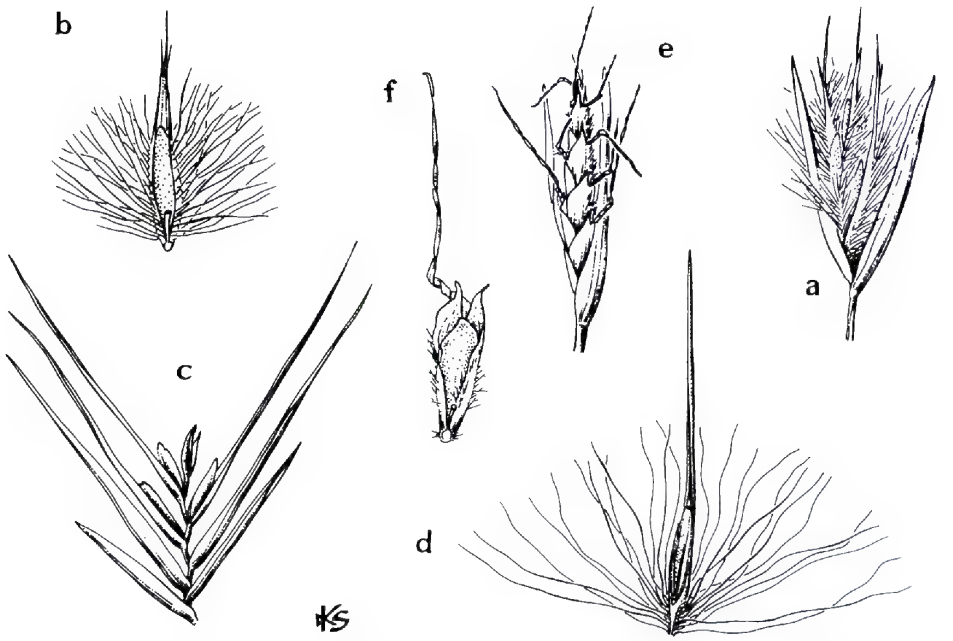

FIGURE 1. Tribe Arundineae, spikelets or their parts. a, b, *Arundo Donax*: a, spikelet, × 3; b, floret (palea and lemma enclosing flower) from adaxial side (note glabrous rachilla segment and hairs along edge of lemma), × 3. c, d, *Phragmites australis*: c, spikelet (parts spread out and hairs omitted for clarity), × 4; d, floret from adaxial side (note abundant hairs from rachilla segment), × 4. e, f, *Danthonia spicata*: e, spikelet, × 3; f, floret from adaxial side (note geniculate awn borne from middle of notch between bilobed lemma apex), × 5.

a short membrane bearing dense fringe of multicellular hairs; blades distichous below, becoming secund above, linear-lanceolate, constricted basally, widest at about ⅓ the length, tapered to a long, attenuate tip, flat, the midvein much wider and thicker than the lateral veins, cross veinlets visible on the abaxial surface. Inflorescences terminal, solitary, plumose, each node bearing several primary branches (1 or 2 of these larger than the others); nodes of the primary branches each with 1 or 2 secondary branches; secondary branches bearing single tertiary branch at each node; inflorescence axis, secondary, and tertiary branches terminated by solitary spikelets; nodes of inflorescence with ring of long, multicellular trichomes (these giving a woolly appearance to inflorescence). Spikelets numerous, lanceolate; glumes 2, unequal, the second shorter than the florets; rachilla pilose, giving the inflorescence a silky or fluffy appearance; flowers 2 to several, the lowest staminate or empty, the succeeding perfect; lemmas lanceolate, long-acuminate, 3-nerved; paleas less than ½ as long as the lemmas. Stamens 3 (lacking, 1, or 2 in lowest, staminate flower); anthers ellipsoid. Ovaries oblong; styles separate, short; stigmas plumose. Caryopses subterete, oblong; styles persistent, indurate; basal furrow broad; hilum ⅓ as long as grain. Base chromosome number 12. TYPE SPECIES: *Arundo Phragmites* L. = *P. australis* (Cav.) Trin. ex Steudel. (Name from Greek *phragmites,*

hedge, probably applied to this genus because of its dense, hedgelike growth along ditches and waterways.)—COMMON REED.

A genus of three (or more) species, nearly cosmopolitan in distribution. The only species in the New World, *Phragmites australis* (*P. communis* Trin.), is widespread, but not especially abundant or common, in the Southeast.

Occurring on all continents except Antarctica, *Phragmites australis* may have the widest distribution of any angiosperm. It was present in the American Southwest at least 1000 years before European contact (Kane & Gross), and in southern New England at least 3000 years ago (Niering & Warren). Reported in 1843 as occasional throughout New York State (Torrey), it was not reported from Georgia or South Carolina by Elliot (1821–1824) and remained unknown in those states until the 1970's (Stalter). It is now abundant in New York, where it may be in part adventive (Mitchell). It spread rapidly on Long Island during the early twentieth century, which may be explained by the introduction of a more aggressive biotype from Europe or elsewhere. Distinctive morphotypes, presumably genetically based, have been reported from southern Louisiana (Schott & White). The complex and confused taxonomy of Old World populations makes it difficult to match the North American populations with any of the numerous European varieties and cultivated forms.

Phragmites japonicus Steudel, $2n = 48$, was recognized by Tsvelev, who distinguished it from *P. australis* by its shorter glumes and spikelets and its zigzag (not straight), elongate rhizomes. The species occurs in Japan, China, and the extreme eastern Soviet Union. *Phragmites Karka* (Retz.) Trin., $2n = 18, 36, 38, 48$, grows in tropical Africa, southeastern Asia, and northern Australia (where its distribution complements that of the more temperate *P. australis*). *Phragmites mauritianus* Kunth is found in tropical Africa and the islands of the Indian Ocean (Fanshawe). The species are barely distinguishable (Clayton & Renvoize).

There is considerable variation in the chromosome complement of *Phragmites australis*. Haslam (1972) reported diploid numbers of 36, 48, 84, and 96. Aneuploids are also reported: $2n = 42, 44, 46, 49, 50, 51, 52, 54, 56$ (Gorenflot *et al.*, 1972). In Europe tetraploids and octaploids account for most populations; hexaploids are rare, being reported from Sweden (Björk), the Mediterranean region, and Iran and Afghanistan (Bahrman & Gorenflot). In the New World hexaploids have been reported from Costa Rica (Pohl). Tetraploid and octaploid clones grow together in the Danube Delta (Bahrman & Gorenflot). No correlation between ploidy, habitat, and geography was found in a survey of 40 European populations (Raicu *et al.*). Apparently the only report from North America is $2n = 48$ from a Canadian population (Hunter).

Bahrman & Gorenflot reported variation in soluble proteins of leaves in an extensive survey of European, North African, and Central Asian populations. Principal-components analysis revealed four major groups on the basis of isozymes present. The diversity of isozymes could not be correlated with ploidal level. The greatest diversity in isozymes was found in populations in Iran and Afghanistan, while the greatest variation in chromosome number was in southern Europe. Evidently, macromolecular diversification in this species has proceeded independently from chromosomal changes.

There are numerous reports worldwide of lack of seed set in *Phragmites australis*. A complete explanation has yet to be provided, and the question offers possibilities for further research. Meiosis is regular in certain populations from France (Cartier & Lenoir). However, chromosome fragmentation during microsporogenesis was detected in populations from Ireland that failed to set seed (Curran). In populations from India, megasporogenesis was normal, but microsporogenesis was arrested at the tetrad stage, and there was no mitotic division to produce the vegetative and generative nuclei (Satyamurty & Seshavatharam). Abundant seed set has been reported in populations from Afghanistan and Iran (Bahrman & Gorenflot), South Africa (Curran), Minnesota (Harris & Marshall), and the Mackenzie District, Northwest Territories, Canada (Cody). In Swedish populations, however, reproduction by seed was limited: only 0.3 –8.0 percent of the florets produced viable seed (Gustafsson & Simak). No viable fruits have been reported from Ontario populations, and reproduction there has apparently been entirely vegetative (Dore & McNeill). Self-incompatibility may account for low seed set because clonal growth has produced genetically homogeneous populations (genets).

Germination is influenced by temperature, with the rate increasing linearly from 16 to 26°C, while the number of days needed for germination decreases from 25 at 16°C to only ten at 26°C. The seeds cannot germinate under more than 5 cm of water. Seed germination is little affected by salt concentrations below one percent, reaching a limit of tolerance at two percent (Kim *et al.*) in Korean populations. Plants of *Phragmites australis* are able to grow in brackish as well as fresh water. Evidently tolerance of salinity varies widely (Hocking *et al.*): a maximum tolerance for mature plants was reported as 1.2 percent in Britain, 2.9 percent in New York, and 4.0 percent on the Red Sea coast.

For detailed reviews of the autecology and physiological ecology of *Phragmites australis,* see Haslam (1972, 1973) and Hocking and colleagues. For a popular nontechnical account of general ecology and economic importance, see Brown.

Plants of *Phragmites* are used by humans in several ways. Stems are used for basketry and thatch in several European countries, and as a source of pulp for paper production, especially in eastern Europe. Immature stems provide forage for cattle in Australia (Hocking *et al.*) and southern Africa. *Phragmites australis* is an invasive weed in the northeastern United States. The rhizomes are able to grow under pavement and cause damage by cracking and piercing it (Amano & Maki; Hocking *et al.*). Unwanted populations can be effectively removed by cutting them several times annually, particularly in midsummer when rhizome starch reserves are lowest. Dense stands provide wildlife habitat in Europe (Bibby & Lunn). Reeds are planted on recently drained lands in the Netherlands and Japan (Kamio) to remove excess water and prepare the soil for agriculture.

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3. **Neyraudia** Hooker f., Fl. Brit. India **7:** 305. 1896.

Caespitose perennials of damp, sunny places. Roots fibrous; rhizomes short, solid. Stems erect; nodes glabrous. Leaves several, cauline; sheath glabrous; ligule membranaceous, pilose (abaxial ligule a conspicuous cartilaginous ridge, pilose, becoming glabrous with age); blade linear-lanceolate, very slightly auriculate, the margin scabridulous, the surfaces glabrous. Inflorescences terminal (and sometimes axillary also), paniculate, much branched, plumose. Spikelets oblong, 3- to 6-flowered; glumes 2, broadly lanceolate, hyaline; rachilla internodes pilose; calluses pilose; lemmas lanceolate, 3-nerved, pilose abaxially toward the edges, the apex bifid, aristate from the notch, the awn scabridulous, stiffly excurved or recurved, sometimes slightly spiraled; paleas lanceolate, hyaline, 2-nerved. Stamens 3; anthers ellipsoid. Ovaries oblong, glabrous; styles 2, free; stigmas short, feathery. Caryopses linear, subterete, slightly dorsiventrally flattened; hilum short; embryo large. Base chromosome number 10. TYPE SPECIES: *N. madagascariensis* (Kunth) Hooker f. = *N. arundinacea* (L.) Henr. (Name an anagram of *Reynaudia,* a monotypic genus of Cuban grasses.)—SILK-REED.

Two species, both endemic to the Old World tropics. One species, *Neyraudia Reynaudiana* (Kunth) Keng, $2n = 40$, silk-reed, Burma-reed, is adventive in southern Florida (Hall; Long & Lakela; several specimens, the earliest from 1930, examined from Dade County). *Neyraudia arundinacea* (L.) Henr., $2n = 40$, a native of southern Asia, has been cultivated in southern Florida (Hall) and might be anticipated as an adventive. In *N. arundinacea* the first lemma subtends a perfect flower, while in *N. Reynaudiana* it subtends a sterile one.

Leaves of *Neyraudia* have an abaxial (external) ligule, which has been overlooked by some workers. It consists of a cartilaginous ridge convergent at its ends with the adaxial ligule. The abaxial ligule is pilose at first but usually becomes glabrous as the leaf matures.

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4. **Danthonia** A. P. de Candolle in Lamarck & A. P. de Candolle, Fl. Franç. ed. 3. **3:** 32. 1815, nom. cons.

Caespitose perennials. Roots fibrous or wiry. Rhizomes lacking. Stems several, unbranched, terete, more or less scabridulous, glabrous or pilose; nodes with a medial constriction. Leaves several to many, basal and cauline; sheath open, shorter than the blade, glabrous or pilose; ligule a dense fringe of short hairs; blade flat (sometimes becoming involute in age), glabrous or pilose, the margin and midvein scabridulous. Inflorescences terminal and axillary (terminal cleistogamous or chasmogamous; axillary cleistogamous, enclosed in sheath); unbranched except for 2–5 primary branches, these appressed or spreading, scabridulous. Spikelets 1–3 per branch, narrowly ellipsoid, 4- to 8-flowered; glumes 2, equal, lanceolate, (3- to) 5- to 7-nerved, acute, mucronulate, persistent; rachilla straight, glabrous; calluses pilose; lemmas elliptic,

5-nerved, pilose abaxially especially near the margin, bidentate, bearing an awn from the notch between the teeth, awn with spiraled base and straight apex (axillary florets awnless); paleas broadly elliptic. Lodicules 2 or lacking, oblong to ovate, entire or truncate. Stamens 3; anthers narrowly ellipsoid, the thecae divergent apically and basally. Ovaries ovoid; styles very short; stigmas 2, feathery. Caryopses oblong to ellipsoid, dorsiventrally flattened (the abaxial face convex, the adaxial concave), the base stipitate, the apex obtuse; embryo about ⅓ as long as endosperm. Base chromosome number 12. (*Sieglingia* Bernh., nom. rejic.; including *Rytidosperma* Steudel, *Notodanthonia* Zotov.) TYPE SPECIES: *Avena spicata* L. = *D. spicata* (L.) Roemer & Schultes, typ. cons. (Named in honor of Étienne Danthoine, early nineteenth-century French botanist.)—OAT GRASS.

A genus of about 80 species (Conert, 1987), here accepted in a broad sense to include the segregate *Rytidosperma. Rytidosperma* was centered in Australia and New Zealand and was treated as a genus, on shaky grounds, by Clayton & Renvoize (but not by Conert, 1987). Reviewing all species attributed to *Danthonia,* Conert found no constant feature to distinguish it from *Rytidosperma.* The patterns of lemma pubescence, often used to distinguish between the two genera, show greatest diversity in Australia. Tomlinson, in an anatomical survey of the tribe, noted that *Danthonia* and *Rytidosperma* are alike in leaf-blade anatomy but differ in lodicule morphology. In *Danthonia* the lodicules lack both macrohairs and microhairs, while in *Rytidosperma* both are present. There are 32 species in Australia (Conert, 1987; Vickery) and 16 in New Zealand. There are two endemics in the Himalayas, two species in Northeast Africa, and 18 species in South America. All the North American representatives of *Danthonia* are $2n = 36$ (Gray *et al.*).

Only three species occur in the Southeast. *Danthonia spicata* (L.) Beauv. (leaf blades involute; panicle branches erect; glumes 7–14 mm long; lemma teeth (not central awn) less than 2 mm long) is widespread, occurring from Labrador to southeastern Alaska, south to western Florida and eastern Texas, and in the mountains of New Mexico and northern California. A disjunct population occurs in Hidalgo, Mexico (Conert, 1987). Canadian populations were recognized by Fernald as var. *pinetorum* Piper, said to differ in having mostly straight (not curled) basal leaves and broader, weakly nerved glumes. Dore & McNeill, however, thought most Ontario populations belonged to the typical variety.

The second southeastern species, *Danthonia compressa* Austin (leaf blades flat; panicle branches spreading; glumes 7–14 mm long; lemma teeth about 3 mm long) occurs from southern Quebec to Ohio and south to the mountains of North Carolina and Tennessee.

The third, and probably the most abundant, southeastern species is *Danthonia sericea* Nutt. (leaves involute, generally silky-pubescent; panicle branches short, erect; glumes 12–18 mm long; longer lemmas 7–10 mm long), which occurs on the Coastal Plain and Piedmont from southern New Jersey and southern Kentucky to northern Florida and Louisiana. It consists of three races, which have been accorded varietal or specific status by some workers. The

major taxonomic problem in the southeastern taxa concerns this species and its segregate *D. sericea* subsp. *epilis* (Scribner) Blomq. (*D. epilis* Scribner; leaves glabrous), reported to be restricted to the upper Piedmont of North Carolina and Georgia. Quinn & Fairbrothers made cytological preparations from 21 populations and found no karyological differences (all were $2n = 36$). Populations of *D. sericea* subsp. *epilis* in New Jersey begin growth and flowering in response to increasing soil temperature and are day-length neutral. However, populations on granitic outcrops in Georgia have their flowering time fixed genetically (Rotsettis *et al.*) and start to flower early in the year, which may be advantageous in allowing seed set before the thin soil in which the plants typically grow dries out in the summer. Gray and colleagues also studied these two regional groups of subsp. *epilis*: populations from bogs in New Jersey lacked stomata and macrohairs on the abaxial leaf surfaces but had them on the adaxial ones, while plants from well-drained sites of the Piedmont and Coastal Plain had hairs and stomata on both surfaces. Some intermediate populations from sites that were intermittently wet had abaxial hairs and stomata, but they were more plentiful on the adaxial surface. All populations had the same chromosome number, $2n = 36$. When grown in the greenhouse, both races responded to decreasing soil moisture by reduction in the width of the stomatal aperture. There is no information on compatibility or sterility between these differentiated populations, so it seems premature to recognize them taxonomically. The potential for further research is enticing.

Five other species of *Danthonia* occur in North America. *Danthonia intermedia* Vasey is boreal and cordilleran in distribution, occurring from Newfoundland to Alaska and south to the mountains of New Mexico and northern California (Cayouette & Darbyshire). It also grows on the Kamchatka Peninsula of the eastern Soviet Union (Conert, 1987; Tsvelev). *Danthonia Parryi* Scribner of the Rocky Mountains (Alberta to Colorado) is morphologically similar and probably closely related.

The second pair of western species is characterized by few-flowered inflorescences. *Danthonia californica* Bol. has an amphitropical distribution, occurring in the West from Montana to southwestern British Columbia and south to New Mexico and California, and is also reported from Chile (Munz). Pilose plants have been segregated as var. *americana* (Scribner) Hitchc. *Danthonia unispicata* (Munro ex Thurber) Munro ex Macoun has inflorescences consisting of only one (to three) spikelet(s). Its range is similar to that of *D. californica*, and Munz considered the two species as doubtfully distinct.

The Australian *Danthonia pilosa* R. Br., $2n = 48$, is adventive in California from seed planted for forage (Hitchcock, 1951; Munz).

Baum & Findlay emphasized lodicule morphology in their revision of the Canadian species of *Danthonia*. They detected four lodicule patterns, two of which are represented in the southeastern species (lodicules were absent from both *D. sericea* and *D. spicata*; club-shaped lodicules—presumably two per floret, although they did not say so—with truncate apices characterized *D. compressa*). Thus they recognized the North American species chiefly by the lodicules, a taxonomic scheme not receiving much if any subsequent acceptance. In a second paper, Findlay & Baum described a new species, *D. cana-*

densis Findlay & Baum, which occurs across Canada and the northern United States, and which differs from *D. Parryi* in the shape of the lodicules and other quantitative characters usable only by means of principal-components analysis. Such "one-character" taxonomy is problematic in a genus beset with taxonomic difficulties (see Rotsettis *et al.*; Vickery).

A notable feature of *Danthonia* is the production of cleistogamous spikelets by some species, including the three southeastern representatives. Cleistogamy was apparently first noted in the genus by Austin, who described "spikes" on short branches wholly enclosed by upper leaf sheaths. Clay (1982) investigated the reproductive biology and population genetics of *D. spicata* in North Carolina. All plants produced both axillary (cleistogamous) and aerial ("chasmogamous"—actually cleistogamous and chasmogamous) flowers,[5] but the proportion of each kind was variable. Using vegetatively produced individuals and growing these under different conditions, Clay (1982) found that plants of the same genotype consistently produced more aerial florets in the greenhouse (40 percent) than in the field (28 percent). Larger plants produced a higher percentage of axillary florets. From genetic analysis of related individuals, he determined that 50 percent of the observed variation in production of axillary florets was genetically based and 50 percent environmentally based. Genetic differences were possibly the result of natural selection. In other natural populations the percentage of axillary florets was lower: eight or nine percent in Wyoming and zero in Michigan (Scheiner & Teeri).

Clay & Antonovics (1985b) also compared genetic variation in certain morphological characters for greenhouse- and field-grown plants of *Danthonia spicata.* They found significant genetic variation present for every character examined, both vegetative (height of flowering stem; length and width of uppermost leaf) and reproductive (number of cleistogamous flowers; length of second glume). The degree of variability among closely related individuals (plants from seeds of the same carpellate parent) suggested that the aerial florets are in part cleistogamous or self-pollinated.

The three southeastern species vary in the relative proportions of aerial and axillary florets (Clay, 1983b). *Danthonia compressa* averaged 50 percent aerial florets (minimum, 35 percent); *D. spicata* ranged from zero to 70 percent, with an average of 25 percent; and *D. sericea,* including plants assignable to *D. epilis,* averaged only five percent (maximum, ten percent). Grazing or mowing appears to favor the production of axillary florets over aerial, since such populations had the highest percentage of axillary florets.

Clay (1983b) compared the weight of diaspores (caryopsis plus clasping lemma and palea) from aerial and axillary florets in the southeastern species. In *Danthonia compressa* the average weight for both kinds was 0.80 mg, while the axillary ones were 25 percent heavier in *D. sericea* and 35 percent heavier

[5]In plants from Durham County, North Carolina, studied by Clay, all aerial florets were apparently chasmogamous. However, Clay sent seeds from his study population to Philipson, who grew them in a greenhouse in New Zealand. About half of the aerial spikelets in the resulting plants were cleistogamous (Philipson, 1986). In the discussions of genetic studies by Clay, I have used the categories aerial and axillary florets where he used "chasmogamous" and "cleistogamous." See discussion below and Philipson for further details, and see Darbyshire & Cayouette for comments.

in *D. spicata*. In the two latter species about two thirds of the difference was due to heavier lemmas and paleas in the axillary florets.

A comparison of the fitness of plants derived from aerial and axillary caryopses in *Danthonia spicata* showed only a slight difference (Clay & Antonovics, 1985a). The advantage in survival was mostly during the seed and seedling stages (Clay, 1983a). Both kinds of diaspores germinate in mid- to late spring in North Carolina. Maximum germination was about 30 percent for seeds stored dry at room temperature for several months. Axillary cleistogenes germinate over a longer period (30 percent germination in ten days) than aerial (10 to 15 percent in 30 to 40 days).

Subsequent studies by Philipson show the diversity of reproductive features in *Danthonia spicata*. She grew 49 plants (122 panicles) from a single North Carolina population and found that 52 percent of the florets from aerial panicles were in fact cleistogamous (rather than chasmogamous, as was assumed by Clay). There was wide variation in the percentage of cleistogamy, and 58 panicles (nearly 50 percent) were wholly cleistogamous. In the aerial cleistogamous florets the anthers were tiny and indehiscent; the pollen grains germinated in situ, and the tubes grew through the anther wall into the adjacent stigmas. Often, both chasmogamous and cleistogamous florets were produced in the same spikelet (the cleistogamous generally proximal to and maturing sooner than the chasmogamous). Thus, many plants produced three kinds of diaspores: chasmogamous and cleistogamous ones from aerial inflorescences, both dispersed some distance by the hygroscopic lemma awns, and atelechoric awnless axillary cleistogenes generally germinating quite close to the parent plant.

Danthonia spicata is able to grow in diverse environments, from open sandy soil in full sun to closed-canopy oak-pine forest with only ten percent of full sunlight in Michigan (Scheiner & Teeri). Individual plants have the ability to recover from severe droughts. Both genetic differentiation (microevolution or genetic drift) and phenological flexibility appear to contribute to this ecological amplitude.

Population variability based on genetics has also been demonstrated in the Australian *Danthonia caespitosa* Gaudich. (Quinn & Hodgkinson). The response to density and to temperature varied along a latitudinal gradient. The infraspecific diversity of species from different regions tends to counter the suggestion of Clayton & Renvoize that the Arundinoideae are not successful and are outside the mainstream of grass evolution.

Seed dormancy in the Australian species *Danthonia carphoides* F. Mueller ex Bentham and *D. caespitosa* was investigated by Hagon. Seeds sown within two weeks of ripening had 30 percent germination. After storage at room temperature (dry) for six weeks, all dormancy was broken. Germination responses were not appreciably affected by temperatures in the 15–35°C range.

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Caespitose annuals or perennials of dry soils. Roots fibrous; rhizomes short or lacking. Stems several to many, erect or slightly oblique, branched from the axils, especially in the lower portion. Leaves several, cauline and basal; sheath glabrous or pilose; ligule a short, pilose membrane; external ligule (sometimes present) a cartilaginous ridge interrupted by the midvein, bearing a row of trichomes; blade linear, about as long as the sheath [absent], involute or flat, the margin and surface scabridulous. Inflorescences paniculate, more or less open. Spikelets pedicellate, 1-flowered; glumes 2, strongly unequal to subequal, sometimes awned; lemmas lanceolate, shorter or longer than the glumes, involute [convolute], 3-nerved, calluses prominent, shortly hispid, the awn conspicuous, scabridulous [plumose], with 2 lateral teeth whose bases are sometimes fused to the lower portion of the awn forming the awn column; paleas much shorter than lemmas, 2-nerved. Lodicules 2. Stamens 3 or 1; anthers linear. Ovaries shortly cylindrical; styles 2, short; stigmas plumose, laterally exserted. Caryopses compressed or terete, tightly enclosed by lemma and palea,

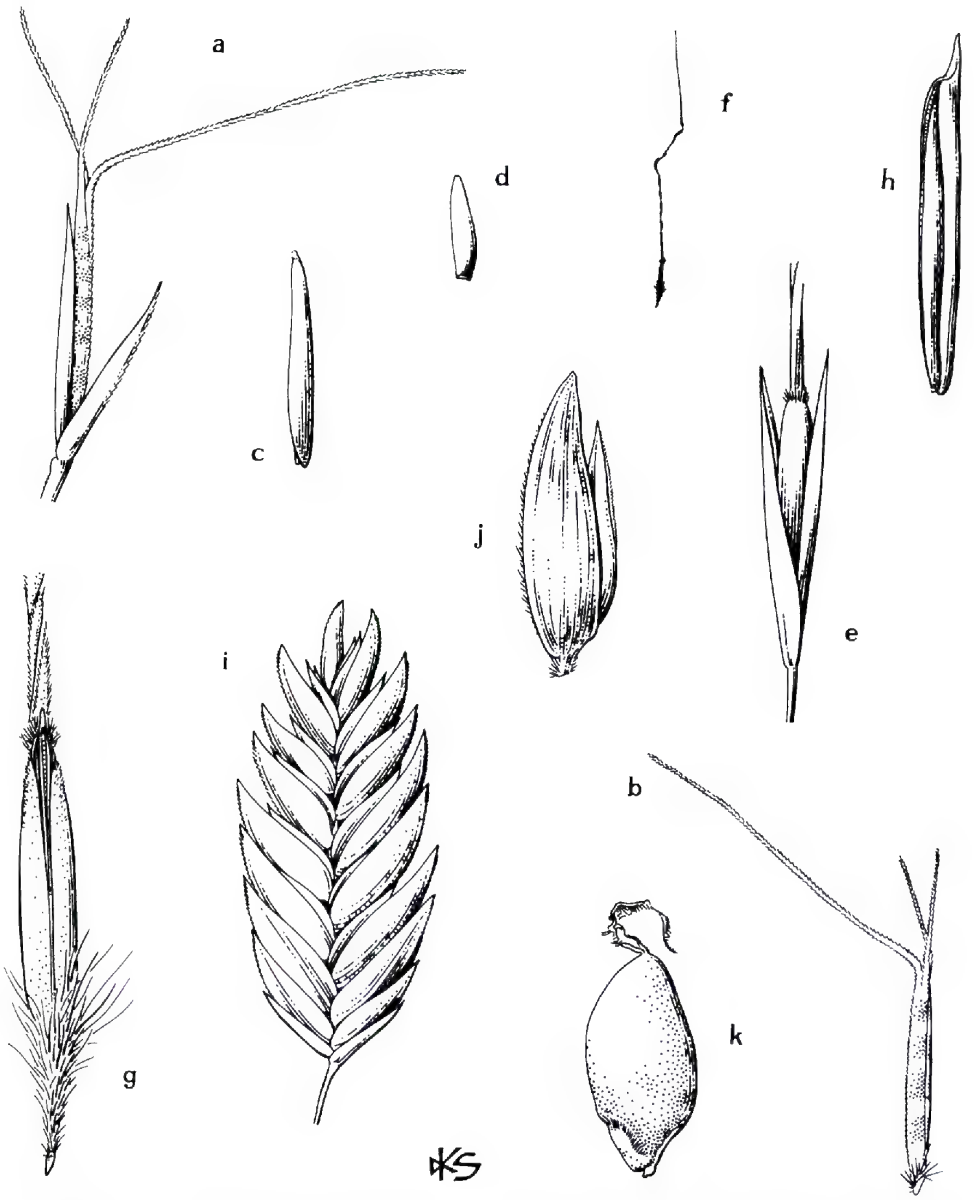

FIGURE 2. Spikelets or their parts. a–d, Tribe Aristideae, *Aristida longispica* (sect. *Aristida*): a, spikelet with glumes spread apart, × 6; b, floret (lemma and palea) containing mature caryopsis, the 3-awned lemma completely enclosing palea and caryopsis, × 6; c, caryopsis, × 6; d, palea, × 12. e–h, Tribe Stipeae, *Piptochaetium avenaceum* (*Stipa avenacea*): e, spikelet with single floret (only basal portion of lemma awn shown), × 2; f, entire floret, showing relative length of hygroscopic lemma awn, × ⅓; g, floret (note hairy base of lemma and rachilla forming bearded, sharp-pointed callus), lemma clasping pointed palea (only base of lemma awn shown), × 5; h, palea, × 5. i–k, Tribe Centotheceae, *Chasmanthium latifolium* (*Uniola latifolia*): i, spikelet, × 1½; j, floret (lemma and palea enclosing flower), × 3; k, caryopsis, × 5.

sometimes longitudinally furrowed. Base chromosome number 11. TYPE SPECIES: *A. adscensionis* L., the only species included in the genus by Linnaeus. (Name from Latin *arista,* a beard or awn.)—THREE-AWN GRASS.

A genus of about 330 species distributed nearly throughout the tropical and warm-temperate regions of the world. Twenty species occur in the Southeast. The genus is reasonably well known, thanks to the worldwide studies of Henrard (1926; 1927; 1928; 1929; 1932; 1933a, b). A synopsis of the southeastern species (including those in Delaware, Maryland, Virginia, West Virginia, and Kentucky) has been presented by Allred (1986). His keys allow easy identification of the species in eastern North America.

The subgeneric classification of *Aristida* is confused and difficult. There are probably parallels in the evolution of spikelet characters noted by Henrard (1926; 1927; 1928; 1929; 1932; 1933a, b). Section ARISTIDA (sect. *Chaetaria* (Beauv.) Trin.) (awns of the lemma persistent) accounts for about 200 species worldwide and 18 of the 20 species in the Southeast. The section was divided by Hitchcock (1924, 1951) into informal groups, a scheme also followed by Allred (1986) and seemingly prudent in view of the lack of understanding of the phylogeny of the genus. About one third of the southeastern species are annuals (group Dichotoma of Hitchcock, 1951), the remainder perennials. A common situation in the section is pairs of intergrading species; for example, *A. basiramea* Engelm. ex Vasey and *A. dichotoma* Michx. Polyploidy characterizes several species of the southwestern United States (DeLisle, 1973) of the *A. purpurea* Nutt. complex (group Purpureae of Hitchcock, 1951). *Aristida Roemeriana* Scheele, $2n = 22$, includes only diploids; *A. longiseta* Steudel, *A. Fendleriana* Steudel, and *A. glauca* (Nees) Walp., diploids and tetraploids ($2n = 22, 44$); *A. Wrightii* Nash, diploids, tetraploids, and hexaploids; and *A. purpurea* Nutt. ($2n = 88$), octaploids as well. In none of these species were morphological criteria found to distinguish the various autopolyploids (DeLisle, 1969). The polymorphic and pantropic *A. adscencionis* L., $2n = 22$, has numerous infraspecific categories. In the New World it has been reported from Texas westward to California and southward through Central and South America.

Section ARTHRATHERUM (Beauv.) Reichenb. (awn column deciduous at its base) is most diverse in Africa. There are only two species in the Southeast. *Aristida desmantha* Trin. & Rupr. (longer glume less than 2 cm long; awn column 2–5(–7) mm long) occurs in our area only in Arkansas and Louisiana. *Aristida tuberculosa* Nutt. (longer glume more than 2 cm long; awn column 8–15 mm long) is widespread in the eastern United States and in all of the southeastern states except Tennessee and Arkansas. Chromosome counts (e.g., *A. brevisubulata* Maire, $2n = 22$, and *A. pallida* Steudel, $2n = 44$) suggest the occurrence of polyploidy in African representatives of this section.

The chiefly African sect. PSEUDARTHRATHERUM Chiov. is not represented in the New World. This section differs from the preceding in having the awn column deciduous at its summit (i.e., just below the level at which the lateral awns branch from the central one).

Also not represented in the New World is sect. STREPTACHNE (R. Br.) Domin

(awn column present, not articulated). This section, recognized by Lazarides and by Bourreil & Reyre, was included without comment in sect. ARISTIDA by Clayton & Renvoize. One of its species, *Aristida Humbertii* Bourreil & Reyre, known from Angola, is unique in the genus in that all three awns are reduced to short mucros.

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Tribe STIPEAE Dumortier, Obs. Gram. Belg. 83. 1824.

6. **Nassella** (Trinius) Desvaux in C. Gay, Hist. Chile Bot. **6:** 263. 1854.

Caespitose perennials. Stems hispid or glabrous; nodes appressed-hispid, becoming glabrous with age (lower nodes usually geniculate). Leaves several to many, mostly basal; sheath pubescent or glabrous; ligule an unfringed membrane (abaxial ligule absent); blade setaceous to linear, more or less involute, hispid abaxially, less so adaxially. Inflorescences solitary, terminal, paniculate; branches flexuous, scabrid, sometimes hairy. Spikelets 1-flowered, slightly laterally compressed, disarticulation above glumes. Glumes 2, equal, broadly lanceolate, acute [awned], 3-(to 5-)nerved. Lemmas elliptic, convolute, becoming indurate, hispid basally, the surface densely covered with short, stout prickles (seemingly tuberculate), contracted into a smooth, basally fringed collar at the base of the awn, the awn 5–10 times longer than lemma, geniculate, scabrid, hairless. Paleas elliptic, much shorter than lemmas (or absent), nerveless, hyaline. Lodicules 2, glabrous, fleshy. Stamens 3; anthers oblong. Ovaries oblong, glabrous; styles free, stigmas 2. Caryopses oblong to pyriform, laterally compressed, smooth; hilum linear; embryo large, with epiblast. Base chromosome number 14. (*Urachne* sect. *Nassella* Trin. Mém. Acad. Sci. St. Pétersb. Sci. Nat. VI. **1:** 73. 1830.) LECTOTYPE SPECIES: *N. pungens* Desv., designated by Parodi (1947). (Origin of name unknown.)

A genus of about 50 species (Barkworth & Everett), in an area from Patagonia north through the Andes into the Caribbean region, Mexico, and the United States, and western Canada. The only southeastern representative, *Nassella leucotricha* (Trin. & Rupr.) Pohl (*Stipa leucotricha* Trin. & Rupr.), Texas wintergrass, $2n = 28$ (Gould), occurs sporadically in western Louisiana and southwestern Arkansas and ranges southward through Texas into South America. It is abundant in Texas, where it is important as a cool-season forage grass.

The caryopses of *Nassella leucotricha* have prolonged, erratic germination. They probably germinate more or less continuously throughout the year, except during lengthy dry spells (Fowler). On the basis of controlled-environment experiments, however, Call & Spoonts characterized the optimal parameters for germination and hypothesized that in central Texas most germination would occur from late September through mid-November and, during mild winters, also from December through February.

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7. **Piptochaetium** J. Presl in K. Presl, Reliq. Haenk. **1**: 222. *pl. 37*. 1830.

Caespitose perennials of dry, open places. Stems branched only near the base, glabrous; nodes glabrous, constricted medially. Leaves several per stem; sheath ribbed, glabrous; ligule longer than wide, membranaceous (abaxial ligule absent); blade linear, flat to involute, midvein prominent, surface and margin scabridulous. Inflorescences solitary, terminal, open, paniculate; branches scabridulous. Glumes 2, equal, lanceolate-acuminate, conspicuously 3- to 5-veined, margin hyaline. Spikelets solitary, 1-flowered, terete. Calluses subulate [cuneate], covered with long, stiff, extrorse hairs. Lemmas narrowly oblong [elliptic], 3-nerved (nerves visible from adaxial surface), coriaceous, often tuberculate above, margin involute, fitting into the sulcus of the palea, apex thickened, scabridulous [spiny]; awn several times longer than lemma body, spiraled (hygroscopic), scabridulous. Paleas lanceolate, slightly longer than the lemmas, sulcate medially, glabrous, the apex protruding between the lemma margins. Lodicules 3. Stamens 3; anthers narrowly ellipsoid. Ovaries cylindrical; stigmas 2, plumose. Caryopses slenderly cylindrical, firmly enclosed by palea and lemma. Base chromosome number 11. Type species: *P. setifolium* J. Presl, the only species. (Name from Greek *piptein,* to fall, and *chaete,* bristle, referring to the deciduous lemma awns of the type species.)—Needlegrass.

A genus of about 30 species. The circumscription follows Barkworth & Everett, and Parodi. *Piptochaetium* is distinguished from other genera of the Stipeae by its grooved palea into which the margins of the involute lemma fit (Barkworth & Everett; Parodi). It is characterized by phloem fibers in the leaf blades, colorless cells between the abaxial epidermis and the bulliform cells, and circular to paradermally rounded vascular bundles (Parodi & Freier).

Only two species are found in the Southeast. *Piptochaetium avenaceum* (L.) Parodi (*Stipa avenacea* L.), $2n = 22, 28$, occurs from Massachusetts to southwestern Ontario (Dore & McNeill) and Michigan, south to northern Florida and eastern Texas. It is known from all the Southeastern States, where it grows in oak or pine woods, along roadsides, and in fields.

Piptochaetium avenacioides (Nash) Valencia & Costas (*Stipa avenacioides* Nash) is endemic to central Florida (Hall; Hitchcock; Wunderlin). It has longer awns (6–10 cm, vs. 4–6) and longer lemmas (12–18 mm, vs. 8–10) than *P. avenaceum* (Hall). The two species are otherwise similar and perhaps closely related, but because of considerable parallelism in the Stipeae (Barkworth & Everett), this is perhaps a premature statement. The range of *P. avenacioides,* although restricted, does not appear to overlap that of *P. avenaceum.*

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Tribe CENTOTHECEAE Ridley, Mater. Fl. Malay Penin. **3**: 122. 1907.

8. **Chasmanthium** Link, Hort. Berol. **1**: 159. 1827.

Single-stemmed or loosely clustered perennials of open woods. Roots fibrous; rhizomes short, approximately horizontal. Stems unbranched or sparingly branched. Leaves cauline, several; sheath glabrous or pubescent; ligule a short hyaline membrane or fringe of hairs; blade linear to linear-lanceolate, scabridulous on veins, otherwise glabrous or sparsely pilose. Inflorescences terminal and/or axillary, open or contracted. Spikelets oblong, laterally flattened, sessile or pedicellate, 2- to 12-flowered; glumes 2, equal or subequal, deltoid to lanceolate, acute to acuminate, conduplicate, 3- to 7-nerved, the midvein often scabridulous; lemmas narrowly oblong, acuminate, acute, or bifid, 5- to 15-nerved, the midvein scabridulous or ciliate; paleas about as long as the lemmas, bicarinate, bulged out near the base, the keel scabridulous. Lodicules 2, lobed-truncate, 2- to 4-nerved. Stamens solitary; anther broadly oblong to linear. Ovaries oblong; styles short; stigmas 2, plumose. Caryopses ovoid to ellipsoid, laterally flattened, asymmetric, the apex subacute, the base cuneate to obtuse; embryo small, less than ½ the length of the grain. Base chromosome number 12. (Excluding *Gouldochloa* Valdés, Morden, & Hatch.) TYPE SPECIES: *C. gracile* Link = *C. laxum* (L.) Yates, the only species included by Link. (Name from Greek *chasma,* open or gaping, and *anthos,* flower.)

A genus of five species, all endemics of eastern North America and all occurring in the Southeast. *Chasmanthium* was long included in *Uniola* (Chloridoideae). Detailed studies by Yates established the affinities of *Chasmanthium* with the Centotheceae and the heterogeneity of *Uniola* as circumscribed by Hitchcock and other agrostologists. All species of *Chasmanthium* are self-compatible (Yates).

Chasmanthium latifolium (Michx.) Yates (large spikelets pedunculate, pendent), $2n = 48$, is the most distinctive species and presumably the least closely related to the others. It is found from New Jersey to Kansas south to the Florida Panhandle and south-central Texas, with outlying populations in central Nebraska and the mountains of northeastern Mexico.[6] It occurs in all of the

[6]Reported from Manitoba by Yates as follows: Canada, Manitoba, Cow Creek Bridge, Stillwater, *Gruver,* 13 July 1936 (NCU). I have examined the specimen, and it is *C. latifolium* as annotated by Yates. However, it is unlikely this specimen came from Manitoba. The printed heading of the label reads "Herb. of Margaret G. Dudley/Winnipeg, Canada." There is no locality called Stillwater in Manitoba. There *is* a Cow Creek Bridge in Stillwater, Payne County, Oklahoma, well within the range of *C. latifolium.* Darwin Gruver is unfamiliar as a collector of Canadian plants to the Canadian botanists with whom I have corresponded. Thus I believe the specimen in question came from Oklahoma, and *C. latifolium* should be excluded from Canada's flora.

Southeastern States. Plants produce both cleistogamous and chasmogamous florets. *Chasmanthium latifolium* is tetraploid, while the other species are diploid.

The four remaining species have more or less sessile spikelets and narrow, spikelike inflorescences. The closely related *Chasmanthium sessiliflorum* (Poiret) Yates, $2n = 24$ (southeastern Virginia to Missouri and Oklahoma, south to central Florida and eastern Texas), and *C. laxum* (L.) Yates, $2n = 24$ (southeastern New York to southeastern Virginia, Kentucky, and southeastern Missouri to central Florida and eastern Texas), are distinguished by their tiny (5–10 mm long) spikelets and purple anthers. In both species the lemma and palea spread, exposing the caryopsis at maturity; this distinguishes this species-pair from the other species of the genus, in which the caryopsis remains covered. *Chasmanthium laxum* differs from *C. sessiliflorum* only in having glabrous rather than pubescent leaf sheaths and collar.

Large sessile spikelets characterize the two remaining species, both of which have more restricted ranges than the preceding species: *Chasmanthium ornithorhynchum* (Steudel) Yates, $2n = 24$, occurs on the Gulf Coastal Plain of western Florida, southern Alabama, and southern Mississippi, to southeastern Louisiana. *Chasmanthium nitidum* (Baldwin ex Ell.) Yates, $2n = 24$, grows on the Atlantic and Gulf Costal Plain of South Carolina, southern Georgia, and central and western Florida. In both the spikelets are 7–18 mm long, and the caryopses are covered completely by the palea and lemma. *Chasmanthium nitidum* has glabrous inflorescence axils and only one sterile lemma per spikelet, while *C. ornithorhynchum* has densely pilose axils and two to four sterile lemmas.

The hybrid *Chasmanthium laxum* × *C. ornithorhynchum* is known from the Gulf Coast region of southern Mississippi (Yates). Hybrid populations are associated with both parental species and have enlarged sterile spikelets.

References:

Under subfamily references see Clayton & Renvoize; Clewell; Hall; Hitchcock (1951); Wunderlin; and Yates.

LINNAEUS, THE CORTEX-MEDULLA THEORY, AND THE KEY TO HIS UNDERSTANDING OF PLANT FORM AND NATURAL RELATIONSHIPS

P. F. Stevens[1] and S. P. Cullen[2]

Linnaeus's ideas on the composition of the various parts of the plant and the generation of plant form by the interactions of these tissues both with each other and with the sap of the plant are outlined. Linnaeus used the analogy he drew between the vegetative plant and the larva of an insect to justify his emphasis on parts of the fructification in the classification of genera; as with insects, he used the adult, rather than the larva, in classification. His thoughts on the relationship between the various appendicular parts of the plant in the context of his theories of prolepsis and metamorphosis are summarized. Linnaeus's ideas of plant form support his theories on the generation of plant diversity by hybridization and are closely connected with his description of plenitude—continuity in a largely macroscopic world of systematically arranged form that also incorporated findings from the microscopic world. Here, as elsewhere, the medulla can be shown to be the seat of life, but only its interaction with cortex allowed stable form to become manifest. Goethe's and A. P. de Candolle's notions of the "metamorphosis" of plants are briefly situated with regard to Linnaeus's ideas, as is the work of some earlier botanists. In the discussion the interrelationship is explored between Linnaeus's different approaches to looking at plants and their significance for an understanding both of his taxonomic work and of his more general thinking about the diversity of life. The ideas of Linnaeus, and especially those of Goethe, on the metamorphosis of plant form are situated at one end of a spectrum of responses to the problem of the comprehension of diversity; Linnaeus's own taxonomic system represents the opposite end. The archaic cast to Linnaeus's cortex-medulla theory is confirmed, although its coherence and explanatory powers are abundantly evident.

Most commentaries on Linnaeus's biological work have focused on his idea that the taxonomically important characters of an organism reflect, or are, that organism's essence, and especially on his arrangement of organisms in a classification using these characters. Any ideas that Linnaeus may have had as to how the form of an organism becomes manifest, and how the diversity of form in the living work is generated and organized, are less frequently discussed. It is usually suggested (see, for example, Stearn, 1957, and Gustafsson, 1985) that Linnaeus was perhaps more interested in simply describing the world than in understanding laws or principles underlying the diversity of form present in

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Journal of the Arnold Arboretum **71**: 179–220. April, 1990.

it. However, it is becoming abundantly evident that this is not an accurate perception of his activities, as perusal of the numerous theses written by Linnaeus and defended by his students shows. Largely using these theses, Guédès (1969) outlined the development of Linnaeus's ideas on plant morphology and development; Larson (1971) emphasized the Aristotelian dimensions of Linnaeus's thought and discussed his ideas on plant hybridization in some detail; and Broberg (1985), in a remarkable article, succeeded in pulling together much of the underlying body of theory in these theses and showed clearly the important synthetic component in Linnaeus's writings. One goal of this paper is to bring together these different parts of the story, emphasizing its botanical dimension in particular. We also hope to deepen the appreciation of Linnaeus's important efforts to develop an understanding of organic form and diversity, at the same time stressing the relationship of his thought to that of his immediate predecessors and successors.

Larson (1971) clearly outlined what is, as he noted, largely implicit in the work that embodies Linnaeus's taxonomic principles, the *Philosophia Botanica* (Linnaeus, 1751a): all genera are natural—the work of nature—and form the foundation of theoretical botany. Such genera were to be recognized by distinctive and constant features in the various parts of the fructification, these being the most essential parts of the plant. To quote Larson (1971, p. 93): "The 'naturalness' of Linnaean genera rests, then, upon assumptions about the principles of activity for the performance of which plants have come into being. The nature of the genus has a narrower sense than 'reality': it is the formative factor in reality."

Cain (1958, pp. 154, 155, quoting Maritain, 1983) suggested that "nature" or "essence," although originally in Aristotelian thought referring to those principles of the activity for which an organism came into being—the final cause—might also be restricted simply to "what a thing is," its visible characters. To quote Larson (1971, p. 93) again, "The simple elements of the fructification, when isolated, and given explicit form, teach the naturalist the characters of the genera spelled out by the hand of God." But between God (a cosmic final cause) and explicit form (formal cause), there are other levels of causality. There is the organism with its role in the community (see, for example, Linnaeus, 1749, 1760b),[3] a local final cause. There are also the material and efficient causes of explicit form, which cause any particular form to be what it is, and it is with these levels of understanding of form in Linnaeus's botanical thought that we are mainly concerned here. Although the focus of this paper is not Aristotelian causality in Linnaean thought, it should be remembered that Linnaeus's biological thought as a whole has a decidedly Aristotelian background (Larson, 1971).

This leads to an underemphasized aspect of Linnaeus's work that he developed most actively after about 1749. He suggested that the "formative factor"

[3]Following authors such as Stearn (1966), authorship of the Linnaean theses is to be ascribed to Linnaeus himself, not to the defendant whose name is on the title page. One of the very few cases where the actual defender of the thesis had some hand in its writing is the important *Gemmae Arborum* (see also below). This thesis alone is cited under its defender, Löfling.

of a plant is the medulla: without the medulla, or when the medulla is depleted, the plant dies; through the medulla, the unchanging essence of the plant is transmitted through successive generations. Interaction of the medulla with the cortex leads to the development of all the parts of the plant from cotyledons to pistils; in the flower, in particular, the medulla interacts successively with the different tissues derived from the cortex, each interaction producing a different part of the flower. Although all these parts other than the pistil come entirely from the cortex, the pistil being largely medulla, they cannot develop without the stimulation of the medulla. The parts of the fructification, which include the flower, are of course the basis of most Linnaean genera.

Ideas such as these are discussed at length in a series of theses, especially *Gemmae Arborum* (Löfling, 1749), *Metamorphoses Plantarum* (Linnaeus, 1755a), *Prolepsis Plantarum* (1760c, 1763), *Fundamentum Fructificationis* (1762b), and *Mundum Invisibilem* (1767a). These theses are often extended justifications for positions Linnaeus only outlined in better-known works such as the *Philosophia Botanica* (1751a) and the tenth and subsequent editions of the *Systema Naturae* (e.g., 1759b, 1767b). They owe much to classic notions of the plant body, in particular those of Cesalpino, whom Linnaeus frequently acknowledged, and through Cesalpino, Theophrastus and Aristotle. They are also intimately linked with complex analyses of the relationships between plant parts, which are little connected with Linnaeus's use of plant structure in his systematic studies.

In these more purely morphological analyses, Linnaeus suggested that there was a fundamental similarity (and often interchangeability) between cotyledons, leaves, sepals, stamens, and the like—in fact, between all the appendicular parts of the plant (this term is used without any implication as to what these structures "really" are) except the carpels, and that exception, as we shall see, holds only in some respects. The observations that Linnaeus emphasized in establishing these similarities were very different from those he used in grouping species to form genera, and genera to form families or ordines naturales, as in the fragments of his natural system. He focused on nonessential variation, adopted what might be called a physiological-balance theory of plant reproduction and morphogenesis, and emphasized a parallel between vegetative and floral buds, and, more generally, a whole variety of "budlike" structures in the plant, including the embryo in the seed. Both his systematic and his morphological studies led to an emphasis on continuity of form, but the forms emphasized were different.[4]

Focusing on these aspects of Linnaeus's thought allows us to understand his later work more clearly and perhaps puts his so-called failure or inability to develop more than the bare outlines of a natural system, the development of which he clearly considered to be very desirable, in a somewhat different light. In addition to classifying all the new material that was being sent to him,

[4]Johann Wolfgang Goethe and Augustin-Pyramus de Candolle are usually considered two of the most important early proponents of ideas concerning the fundamental similarity of all plant parts, although the former had little immediate influence in systematic botany (see Guédès, 1969; Cusset, 1982). C. F. Wolff outlined similar ideas in 1766 (Mueller, 1952).

Linnaeus was developing ideas very different from those we commonly attribute to him. Gustafsson (1985, p. 126) noted, "For Linnaeus the crucial aspect of his work (and the only way in which he could, under the assumptions and axioms of his time, proceed) consisted in observing differences in nature at the cost of the similarities. That is, he stressed the *hierarchic* aspect and was forced to ignore *continuity*." He went on to discuss the attempt to depict the chain of being as a specially constructed analytical language. Even if, following Gustafsson, such an attempt is deemed in principle impossible, we see Linnaeus effectively dealing with continuity in his *morphological* work, and he of course adumbrated the problem of continuity in the context of his natural system (e.g., Linnaeus, 1751a; see especially Broberg, 1985). Between Linnaeus's more or less analytical system and his belief that God's handiwork was visible in the natural world lies a complex and incomplete set of theory and observation that explains at an intermediate level organic form in the botanical world. It is centered on the ancient idea that the plant body is made up of cortex and medulla, and it emphasizes continuity. Here Linnaeus's "passion for synthesis" (Broberg, 1985, p. 179) finds its full expression.

Below we outline the different aspects of this "passion for synthesis," treating each more or less separately. These aspects are cross-referenced to indicate the interrelationship of the several strands of Linnaeus's thought that together form a skein of considerable intricacy.

THE CORTEX-MEDULLA THEORY OF PLANT CONSTRUCTION

INTRODUCTION

The cortex-medulla theory of plant construction, in which all parts of the plant are equated with tissues derived from the cortex, or with medullary tissue, first figured prominently in Linnaeus's work in the thesis *Gemmae Arborum,* defended by Pehr Löfling in 1749. Although mentioned in earlier works, it was there always in a much less central position. Löfling's thesis coupled the classical conception of the flower in which the outer, vegetative cortex splits to reveal the inner tissues of the plant with an extensive, but sketchy, elaboration of the cortex-medulla theory. Löfling drew an analogy between the vegetative parts of the plant and the larva of an insect; he looked at budlike structures in general and considered them to be directly comparable; and he examined in some detail the growth of floral and vegetative parts of the plant, entertaining the notion that at least some flowers were precociously developed shoots. This leads to the idea that the parts of the plant other than the stem and root (i.e., all the major organs borne on the shoot) are fundamentally equivalent.

It is interesting to note that this thesis is one of the very few in which the student defending it is supposed to have had an appreciable part in its writing.[5]

[5]This student, Pehr Löfling (1729–1756), also helped to write the *Philosophia Botanica* (Linnaeus, 1751a) at Linnaeus's dictation, Linnaeus being unwell at the time. There are further developments in the ideas mentioned above in this book. During dictation, Löfling questioned things he could not understand, so becoming throughly grounded in Linnaean botany (Blunt, 1971; see Löfling, 1758, p. [3] of the *Företal* written by Linnaeus). One of Linnaeus's best and favorite students, Löfling unfortunately died young while collecting in South America.

PROBLEMA BOTANICUM

in gratiam D:NI AUCTORIS propoſitum

A

PRÆSIDE.

I. Corpus VEGETABILE conſtat *Medulla*, veſtita *Ligno*, facto ex *Libero*, poſtquam ſeceſſit ab interiori ſubſtantia *Corticis*, qui ipſe *Epidermide* induitur.

2. *Medulla* cum tegumentis creſcit ſeſe in longitudinem præprimis extendendo, fibrasque in latitudinem verſus Folia protrudendo.

3. Fibræ medullaris extremitas per corticem protruſa, ſolvitur ſæpius in *Gemmam* ex foliolis imbricatam.

4. *Folium* expanditur attrahendo ſuccum nutritium, quem modicum gemmæ concedit, antequam cadit, nunquam renaſciturum.

5. *Gemma* (3) compendium futuræ herbæ extenditur in ramum, hic in ramulos, inque infinitum, donec fructificatio imponat ultimum terminum antiquæ vegetationi.

6. *Calyx* fit intra gemmam ex foliis non ſecedentibus, deficiente vi eadem removente expandenteque; probant hoc *Nigella*, *Roſa*, *Diapenſia*, *Perianthium cõmune*, *Involucrum*, & ex *Salicis* amento infectifera *roſa*.

7. Hoc facto rumpitur intra calycem ramuli apex, ſecundum leges cuique ſubſtantiæ (1) proprias, inque *Florem* expanditur annuo ſpatio præcocius.

8. *Corollam* teneram, magis mollem & caducam oriri ex corticis, nunc Calycis (6), propria ſubſtantia, pulpoſo libero, confirmant *Flores vernales*, præprimis *Daphnes*, eo tempore, quo Liberi ſubſtantia a cortice non receſſit.

9. *Stamina* fieri ex ſubſtantia lignea (1), olim libero, probat *conſiſtentia*, *ſitus*, *plenitudo* florum e vegetatione vegetiori, ubi ex molli libero indureſcere lignum non permiſit fortior propulſio.

10. *Piſtillum* centri floris, ex propria eaque medullari ſubſtantia ortum eſt, cum alia hoc in loco ſuperſit nulla.

11. *Fructus* ex piſtillo medullari nequit vitam novæ plantæ inchoare, niſi prius ſtaminum eſſentia lignea abſorpta fuerit ab humore medullari piſtilli.

12, Quæ itaque cauſſa connexionis foliorum in Calycem?
quo ramuli apex præcocius rumpatur in florem?

Quæ vis mirabilis hujus effectus?

Nodum extremum vegetationis videtur mihi ſolviſſe, qui hunc explicet Gordium.

FIGURE 1. Linnaeus's questions in the thesis *Gemmae Arborum* (Löfling, 1749, facing p. [i]).

There is, however, a further complication that makes the authorship of the ideas in this thesis uncertain. Facing the first page is a series of 11 aphoristic statements concerning plant construction and development and a final series of questions addressing the forces involved in the phenomenon of flowering. This page, headed "Problems in botany proposed to the glory of God by the president [Linnaeus] of the author [Löfling]," is placed at the end of the reprinted versions of the thesis (e.g., Linnaeus, 1751b, 1786) and has largely been overlooked (but cf. Stafleu, 1971). A reproduction of this crucial page is given here (see FIGURE 1), and a free translation follows.

1. The VEGETABLE body is composed of the *Medulla,* covered by *Lignum* [wood], made from *Liber* [phloem and cambium], after it separates from the inner substance of the *Cortex,* which itself is overlain by the *Epidermis.*

2. The *Medulla* with coverings grows by itself, extending mainly in length and pushing out fibers to the side toward the leaves.

3. The extremity of the medullary fiber protrudes through the cortex, often being broken up in the imbricate *Bud* [made up] of small leaves.

4. The expanded *Leaf,* attracting nutritive sap, which, before it falls, allows a modicum to the bud, never being borne again.

5. The *Bud* (3), the compendium of the future vegetative plant being extended into a branch, first as a twig, then to infinity, up to the time when the fructification imposes the final termination of the growth of the old plant.

6. The *Calyx* being within the bud, [made up] of leaves that do not separate, lacking the force to separate and expand; *Nigella, Rosa, Diapensia, common Perianth, Involucre,* and *Salicis* amento insectifera *rosa* demonstrate this.

7. In this way the apex of the branch is torn apart within the calyx, the substances (1) [the tissues of the plant] following laws that are proper, I say the *Flower* expanding a year precociously.

8. The thin corolla, very soft and caducous arising from the cortex, now [part] of the Calyx (6), the true substance, fleshy liber, *spring Flowers,* especially *Daphne,* confirm at that time when the substance of the Liber does not separate from the cortex.

9. The *Stamens* being derived from the woody substance (1), once liber, the *existence, position,* the *completeness* of the flowers from more vigorous plant show, where the hardened lignum did not allow stronger propulsion from the soft liber.

10. The *Pistil* of the center of the flower, [made] from its special substance of the medulla, with nothing else remaining in that place.

11. The *Fruit* from the pistil [made up] of the medulla is unable to lay the foundations for the life of the new plant, unless first the woody essence of the stamen is absorbed by the medullary humor of the pistil.

12. What then [is] the cause of the joining of the leaves in the Calyx? by what is the precocious apex of the plant torn apart in the flower?

What miraculous force does this?

It appears to me that the ultimate node of the plant is dissolved, as was loosened the Gordian [knot].

The contents of this introductory page outline many of the points that Linnaeus developed over the next fifteen years. It is interesting, and perhaps relevant in attempts to understand authorship of the various parts of this thesis, to note that the emphasis on those forces in the plant that might account for the morphological phenomena observed is not so evident in the body of Löfling's thesis. This, however, is clearly seen to be the central point at issue, as the emphasis on the final statements, possibly written by Linnaeus himself, suggests.

The Basic Construction and Development of the Plant Body

Linnaeus (e.g., 1751a) consistently divided the plant body into three basic parts: the *radix,* or root; the *herba,* or vegetative region of the plant, sometimes simply called "planta" (e.g., Linnaeus, 1741, p. 12); and the *fructificatio,* everything from the calyx to the seed.[6] The root, which took up food from the soil, produced the vegetative part of the plant as well as the fructification. The plant body as a whole was made up of a central medulla, roughly corresponding to the pith, covered by the lignum (wood). This latter arose from the liber (inner bark: phloem and cambium), which was in turn derived from the cortex, itself overlain by the epidermis (see Table 1). These several tissue types could be reduced to two, the cortex and the medulla (Linnaeus, 1759a, p. 4; the "corporea externa" and the "medulla interna" in Linnaeus, 1767b, p. 7), by emphasizing that the lignum and the liber were both derived from the cortex.

In Linnaeus's taxonomic analyses the fructification was divided into two parts, the flower and the fruit, the former being made up of calyx, corolla, stamens, and pistil, and the latter of pericarp, seed, and receptacle (e.g., Linnaeus, 1751a). Linnaeus had very early integrated some of the organs of the fructification with the cortex-medulla division of plant tissue (see Table 1). He thought that the thicker outer cortex formed the calyx, and the thinner inner cortex, the petals; the stamens came from the wood, and the pistil from the medulla (Linnaeus, 1738; see Figure 2A). Thus the inner parts of the plant were displayed by the splitting of the cortex in the flower (see, for example,

[6]Initially the "planta" was thought of as being composed of the trunk, the leaves, the "fulcra" (stipules, prickles, and the like), and the fructification (Linnaeus, 1736a, p. 7).

Table 1. **The main organ categories of the plant and their origin.**

Main plant parts			Tissue types	
Main categories		**Organs**	**Normal arrangement**	**Linnaeus, 1746†**
Radix	Root	Root	Cortex + medulla	—
Herba (planta)	Vegetative plant	Stem	Cortex + medulla	Cortex + medulla
		Leaf	Cortex	Cortex
		Thorns, etc. ("fulcra")	Presumably cortex	Presumably cortex
Fructificatio	Flower	Calyx*	Cortex	Outer cortex
		Corolla*	Liber	Inner cortex
		Stamens*	Lignum	Alburnum
		Pistil*	Medulla	—
	Fruit	Pericarp*	—	Lignum
		Seed*	Medulla‡	Medulla‡
		Receptacle*	—	—

*The seven parts of the fructification.

†This is closer to Cesalpinian ideas as to the equivalence of organ categories with tissue types, see below.

‡The cortex became involved in the production of the seed via the process of fertilization.

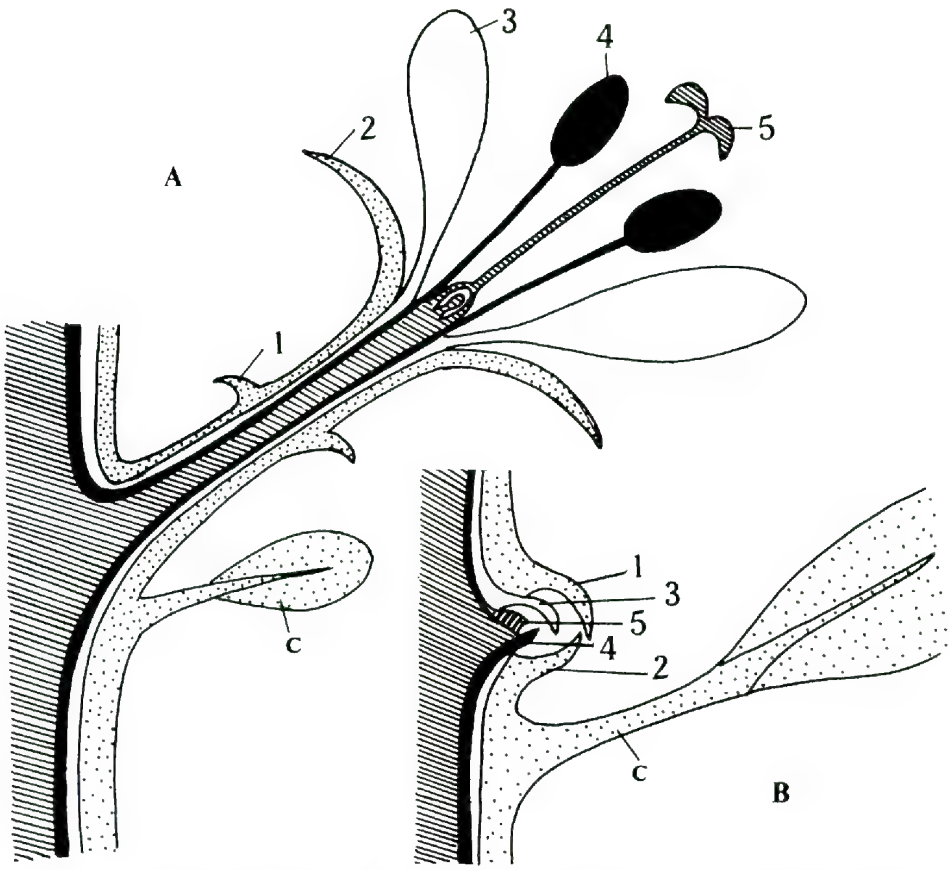

FIGURE 2. Linnaeus's ideas on the construction of the plant body: A, flower; B, vegetative bud (stipple = cortex, black = liber, white = wood, ascending diagonal lines = membranes surrounding medulla, descending diagonal lines = medulla. 1 = first year's growth, 2 = second year's growth, and so on; c = leaf on current year's growth). In flower all growth occurs in a single year (anticipation), in vegetative bud it occurs over several years; for diagrammatic purposes, a single leaf represents each year's growth.

Löfling, 1749, p. 13, footnote s; Linnaeus, e.g., 1755b, p. 5). However, the exact details of this oft-repeated comparison differed. After equating the various organs of the flower with those of the vertebrate reproductive system, Linnaeus (1746) briefly mentioned that the calyx was made up of outer cortex, the corolla from inner cortex, the stamens from nutritive alburnum (sapwood, corresponding to the liber), the pericarp from ligneous substance, and the seed from medulla. Here both parts of the fructification, flower and fruit, derive from the several parts of the basic tissue system of the plant, but usually it was the flower alone that was compared with these tissues (see FIGURE 2A; Löfling, 1749, cf. facing p. [1] and p. 13; Linnaeus, 1751a, 1751c (the medulla produces the seed), 1755a, 1759b). If bracts were included in this comparison, they, too, were considered to be formed from the cortex (Linnaeus, 1763).

In the vegetative plant the ends of the medullary fibers protruded through

the cortex, liber, and wood and stimulated the formation of leaves from the cortex (see FIGURE 2B). The young leaves formed imbricate buds with medulla in the center; the buds themselves did not develop from leaves. Thus the vegetative region of the plant was effectively an assemblage of buds, a composite, or—in modern terminology—a modular organism, that could repeat itself *ad infinitum* unless terminated by the fructification (Löfling, 1749) or the death of the medulla. The medulla was both the form-generating part of the plant and the part that ensured the plant's continued growth; all parts of the plant with the potential for growth had medulla.

Linnaeus (1763) expanded this point in the thesis *Prolepsi Plantarum.* Each of the numerous buds on a tree contained medulla, which, growing out and dividing incessantly, continued the life of the plant, the ultimate fibers of the medulla being in the next generation of buds. Thus, only a few years after a willow twig is put in the ground, the subdivision of the medulla in the buds of that original twig results in a large, copiously branched tree from which twigs can be plucked and planted; the whole process can then repeat itself. In an annual plant, on the other hand, Linnaeus thought that there were no buds, only flowers in the axils of the leaves. This meant that the medulla in each axil was used up in the production of the flowers; the plant then died since it had no medulla left (Linnaeus, 1760c). Hence the only difference between annuals and perennials was that in the former the medulla was quickly used up in the fructification, while in the latter it was for the most part retained in the trunk or root and could produce more buds.

Linnaeus's concept of plant growth contained two antagonistic tendencies or movements involved in growth and development. A movement from the outside of the plant that was manifest in the direction of development of the cortex-derived tissues was nutritive and descending, while that from the inside to the outside was ascending and generative: "the life of the medulla, spongy, divisible by multiplication and with an infinity of endings, growing upwards, incarcerated in the Cortical *Body,* which is nutritive, descending, joined to the ground . . ." (Linnaeus, 1759b, pp. 826, 827; there are extended comparisons with animals in several places—e.g., Linnaeus, 1751a, 1759a). The cortex could be compared to the vascular system; the mouth, or ventricle, of the plant was in the ground, from which the roots drew up nourishment that was purified in the leaves. As elsewhere in this theoretical edifice, there are problems in the interpretation: the force in the cortex is descending, but food is taken (ingested) from the ground. In any case these forces do not exactly correspond to other visualizations of the plant: the three main morphological subdivisions of the plant body are root, vegetative plant, and fructification (see TABLE 1).

In the seed, which was the rudiment of the new plant, the plumule was the scaly, ascending part of the corculum (the plumule-radicle junction and, to many classical authors, the "heart" of the plant). When bathed in sap (humore), the bud could grow *ad infinitum.* The rostellum was the simple, descending part (Linnaeus, 1751a). The above-ground plant was produced from the root. Nothing new was formed; instead, there was simple continuity through the medulla ("Nova *creatio* nulla, sed *continuata* generatio, cum *Corculum* seminis constat parte radicis medullari": *ibid.,* p. 38). As will be seen, the balance of

the upward and downward forces in the plant affected the *kind* of organs it produced, especially whether they were floral or vegetative. The particular *form* of each organ was a manifestation of the essence of the species, although taxonomically unimportant details were due to accidental causes such as a change in the environment or the growth of galls.

Linnaeus returned to the interaction of these tissues with each other and the growth forces of the plant in numerous works (e.g., Linnaeus, 1759a; 1759b, p. 827, translated below; 1767c):

> the plant with the rootlets sucking the humid envelopment (tincturam aquosam) of the ground, which by the heat [that] is daily added, is pushed through the *cortex,* whence the nutrition of the plant, breathing out the superfluous, deposits *liber* on the inner surface ("pariete"), every year separating as *woody* substance, holding up the ascending stem, within which the multiplying *medulla,* the base dissolving, the apex infinite, although I conceive the bundle of fibers as a growing isosceles [triangle], in which stronger force tears apart the outer fibers, diverging outward and penetrating the cortex, terminating in a bud that multiplies similarly; from the obstacle of the cortex appear the expanded leaf, breathing air, looking at the sun, exercised by the movement of the wind, never to be born again; where in truth the force being less driven, the medullary fibers converge, and in protruding they lay bare the substance of the cortex in the *calyx,* of the liber in the *corolla,* of the wood in the *stamen,* of the medulla in the *pistil,* the plant ending in new life, the collected threads in the *seeds* are the last of the medulla.

Thus the medulla was indeed involved in the generation of all the appendicular organs. The leaves could not reproduce themselves or give rise to buds; when a bud, containing medulla, was removed, leaves would never be produced again (see above, also Linnaeus, 1760b). Leaf, petal, and stamen alike were dependent on medulla for their existence, although their substance was cortical in nature. In a very brief summary of the growth of the plant, Linnaeus (1751a, p. 301) even suggested that the whole vegetative part of the plant above the ground (herba) was the product of the medullary substance of the root.

The Analogy between Larvae of Insects and the Vegetative Organs of Plants

Löfling (1749) described the bud as being the larva of the herb—i.e., of the vegetative part of the plant. Linnaeus quickly developed this analogy. There was a metamorphosis in the plant, like that recorded by Jan Swammerdam in cabbage white butterflies: the caterpillar pupated; later the pupa or chrysalis broke through the cortex and metamorphosed, and the butterfly, the perfect form of the insect, emerged (Linnaeus, 1749). Note that this and other analogies Linnaeus used go far beyond mere comparability; they betoken more what we would think of as homologies (Stevens, 1984a, 1984b; Broberg, 1985; see especially Beer, 1983, chapter 3, and Atran, 1990, including references).

> And so it is and will be true, that whoever wishes to understand plants correctly, to understand them from their internal structure, to understand them in the same way as insects, should expect their metamorphosis. For example, whoever should carefully examine *Brassica oleracea,* and afterwards should see *Crambe maritima,* would be quite convinced that *Brassica* and *Crambe* by relationship

> ("cognatione") should border near one another, and never think other than two so very dissimilar[7] plants should produce similar fructification, would, however, suppose the opposite when the fructification appears in *Crambe,* which differs so very much from that in *Brassica* that it comes close to *Rapistrum maximum rotundi folium monospermum Cornuit,* to such a degree that these two, although dissimilar, more properly are cognate and are themselves associated by qualities, more than the aforesaid, and this the internal structure of the plants, placed in front of our eyes in the fructification, shows.
>
> —Linnaeus (1755a, p. 15)

Thus larvae, effectively equivalent to the vegetative, external part of the plant, could be very similar, masking taxonomically important differences in the internal structure of the plant as manifest in the flowers. Other examples were Compositae with rayed flowers and those lacking rays, but which were very similar vegetatively, including *Conyza bifrons* and *C. raguzina, Bidens cernua* and *Coreopsis bidens,* etc. (Linnaeus, 1755a). Linnaeus observed that such plants were called "Bifrontes" by botanists; the *Conyza bifrons radiata* of the first edition of the *Species Plantarum* (Linnaeus, 1753) became the *Inula bifrons* of the second and subsequent editions. Since the petals, stamens, and stigma were at the same time the internal structure of the plant and the adult plant that became visible after its metamorphosis, this disposed of potential objections that the parts of the fructification, on which classification was based, were transient structures. They were not, because they were manifest during the whole life of the *adult* plant, or at least a good part of that life (see Ray, 1696; Sloan, 1972).[8]

The significance of this set of analogies is clear. This way of visualizing the plant meshed with Linnaeus's statements as to the relative importance for classification of the different parts of the plant. The external form of the plant, its habit, was largely the impression on our senses made by its most obvious parts, the stems and leaves, which were cortical in nature. The habit was comparable to the larva and was a poor guide to taxonomic relationships at the generic level. This is because what is classified is not the larva, crust, or skin—not the vegetative parts of the plant derived from the cortex—but the imago, or fructification, generated by the medulla or the interaction of the medulla with the cortex (see, e.g., Linnaeus, 1762b). It was the inner parts of the plant that were displayed in the flower. Following Linnaeus's basically Cesalpinian appreciation of the principles of life, it is in these parts that the vital principles of the organisms resided (see below), and so it is on them that classifications should be based. The fructification became evident only after the metamorphosis of the plant, the calyx, or cortex, being torn. Of course, although all the parts of the fructification were essential taxonomically, when they fell from the plant the essence of the plant had not been lost, since the

[7]Later (Linnaeus, 1759c) corrected to "similar."

[8]To strengthen the analogy, Linnaeus frequently described the fructification as the "animalcule" of the plant, with the calyx corresponding to the elytra, or wing cases, the petals to the wings, and the stamens and pistils to the genitalia (see also Linnaeus, 1759b, 1760a, 1762b, 1767c, 1776).

medulla, which produced them or stimulated their production, persisted in the seed. Hardly surprisingly, then, the seed, with its corculum nestling between the upwardly growing plumule and the downwardly growing radicle, and enclosed by cortical layers that were "sloughed off" or "molted," was the real seat of life in the plant.

The bud, and indeed vegetative variation in general, was of little taxonomic importance at the generic level (Linnaeus, 1762b). However, as Linnaeus later (1767b, p. 10) remarked, the differentiae of the larvae—that is, vegetative differences—could be used for the names of species since such differences were used in distinguishing between species.

Prolepsis, or Anticipation, and the Comparison of Floral and Vegetative Shoots

Despite the variety of form manifested by the appendicular organs, both within and among plants, there were nevertheless important similarities among these organs. One of the ways of looking at such similarities was the theory developed by Linnaeus in which the growth of the flower, which occurred in a single year, could be equated with several years' growth of the vegetative plant. The two theses in which this subject was most extensively treated are *Prolepsis Plantarum* and *Prolepsi Plantarum* (Linnaeus, 1760c, 1763)—literally, the anticipation of plants. These theses, although with similar titles, differ in the approaches that Linnaeus adopted. In the first (Linnaeus, 1760c), defended by Ullmark, emphasis was placed on the fact that each type of floral organ could be considered as equivalent to a year's growth of the vegetative shoot and were themselves the "shoots" (soboles)[9] of that year's growth. In the second (Linnaeus, 1763), defended by Ferber, more emphasis was placed on what is basically a physiological explanation for the relationship among the different parts of the plant in general, the parts of the branch and bud, and the parts of the flower, as well as the tissues out of which all the parts of a branch, bud, and flower are constructed. Of course, instances that apparently did not fit this general explanation received special attention.

However, the notion of the opening of the flower anticipating several years' growth of the vegetative shoot was itself anticipated in earlier writings. In Löfling's (1749, pp. [1], 4) pivotal thesis a similarity among bud scales, cotyledons, and calyx was noted; all enclosed younger parts of the plant and were forced open, or fell off, as they expanded. The plant growing by vegetative buds was like a polyp, and that growing from seeds ("generatio") more like an animal with eggs (see also Linnaeus, 1746). Linnaeus (1759a) later described three types of reproduction in plants; the third was vivipary, itself a kind of precocious growth (see also Linnaeus, 1760a). The bud was simply a continuation of plant, rather than something new; the seed, however, was entirely new when grown

[9]Linnaeus used the term "soboles" in connection with the development of leaves, sepals, petals, and the like, but these are not branches or twigs, for which he used the words "ramus" or "ramulus." Here the word "sobol" is translated as "shoot," and the word is always in quotes; without quotes, the word is used to mean a young branch.

(Löfling, 1749, p. 4, "continuata" and "propagata"; see also Broberg, 1985). However, as is apparent above, both flowers and vegetative shoots were enclosed in buds, the scales of which fell off, and were actually formed in the preceding year (Löfling, 1749). Flowers in the axils of the scales of a catkin (ament) could thus be compared to small buds in the axils of leaves of a leafy shoot, the latter, however, developing ("germinandis") only in the following year (see also Guédès, 1969). Buds were not found in leaf axils where there are fructifications, hence Linnaeus thought about how the fructification, just like the vegetative plant reduced to rudiments ("in compendium redacta"), could develop from a bud that had undergone metamorphosis (Löfling, 1749, pp. 12, 13).

Thus the fructification could develop a year before comparable structures on a leafy branch. Annual plants, too, were precocious (*ibid.*, p. 12): "If precocious flowers, which may be considered to be unexpanded buds, mature seeds in that year [in which they flower], and the same year are dispersed onto the ground, and may germinate in the following year, you may see nature hastening to open the outer bud scales of the fructification to such a degree that germination from the seed corresponds completely to the germination of leaves [which give rise to the developing leaves of the vegetative bud]; herbs ["herbae"] therefore avoid undergoing both vegetative and reproductive growth at the same time." The seed is in some way the "bud" of the annual plant; perhaps this comparison was in part to circumvent the apparent absence of buds in annuals (see Ray, 1686).

Here we see the idea of anticipation combined with that of the metamorphosis or change of one part into another; this latter concept we shall deal with shortly. Both in turn are combined with intimations of the physiological kind of explanation that Linnaeus would later adopt for them. As Löfling (1749) noted elsewhere in the same thesis, buds were nothing but the vegetative part of the plant contracted because of a deficiency in the vegetative force.

There is a very terse summary of the mature version of the theory of anticipation in the important tenth edition of the *Systema Naturae* (Linnaeus, 1759b, p. 826; see also Guédès, 1969): "The 'shoots' of the *present* year are the leaves; of the *next* are bracts; of the *third* the perianth (calyx); of the *fourth* the petals; of the *fifth* year the stamens, and the stamens being produced (exhaustis), the pistil. These things are clear: of themselves; because of Ornithogalum; luxuriant [growth]; proliferous flowers; doubled flowers and Carduus."

A slightly more expanded account appeared soon after in the edition of the thesis *Metamorphosis Plantarum* prepared by Linnaeus for the collected edition of these theses defended by his students, the *Amoenitates academiae* (Linnaeus, 1759c). It should be noted that this account (see FIGURE 3) is an addition and is not found in the original version (Linnaeus, 1755a; 1759c, cf. p. 372). Much of this addition was translated (into French) by Guédès (1969), who did not realize that it was not part of the thesis as originally published.

Linnaeus inserted this new section after discussing "budding" and individuality in *Taenia,* polyps, and the like (see also Linnaeus, 1748). After making an analogy between the cerebral and vascular systems of an animal and the medulla and cortex of a plant, he compared the various parts of the flower

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quadrupeda vivipara pullos ſuos generent, qui utero funiculo umbilicali & placenta alligantur, quæ in illis marceſſit, ſed in vermibus, & quidem inprimis *Tænia*, videmus matrem partum ſuum edere, eidemque adhærere, quo fit, ut pro quavis generatione, novus exoriatur articulus, qui diſtincta eſt vita, ſeu diſtinctum individuum, ut in radice *Tritici repentis*. His intellectis *Polypos* ſeu *Sertularias* inſpicere debemus, qui eodem modo ac Tænia partus ſuos, licet plures, edunt, & iis adhærent, ut ramoſæ plantæ ſimiles evadant; quam primum enim matres moriuntur, indurantur eorum corpora, & truncum vel ramum conſtituunt, adeo ut pulli viventes in ſummitatibus tantummodo ſint, conſimiliter ac in vegetabilibus, in quibus quævis gemma novam conſtituit vitam, licet cum priori cohæreat; ſed fato illi obnoxia eſt, quod, poſt ſemel peractam floreſcentiam vel exuitionem larvæ, nunquam ex eadem, planta aliqua nuda, vel flos proveniat.

Uti Animalium machina conſtat Syſtemate *cerebroſo* & *vaſculoſo* nutriente, ſic etiam vegetabilium; in his *Medulla* loco cerebri ſ. Medulla ſpinalis & *Cortex* loco vaſorum per quem ſuccus alimentaris defertur. Ex cortice deponitur quotannis Liber, ex Libro fit Lignum rigidum loco oſſium. Adeoque hæ duæ partes eſſentiales conſtituunt Larvam plantarum & hæ partes dein mutantur in Florem, tamquam in Inſectum volitans coleoptrato calyce corticali, alatis Petalis e libro licet fixis, maſculis Staminibus e ligno & femineo Piſtillo Medullari.

Quomodo hæc metamorphoſis fiat vel non fiat apertiſſime patet intuenti e. gr. Scillam aut Ornithogalum capenſe. Ubi

a. Bulbus conſtans ſquamis tunicatis, prioris anni relictis baſibus foliorum.

b. Fo-

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b. Folia baſi intra bulbum vaginantia præſentis anni ſoboles & herba ſunt.

c. Gemma minima reſidet intra baſin ſinguli folii in bulbo.

d. Hæc gemma (c) dabit proximo inſequente anno folia, niſi tabeſcat.

e. Si vero hæc gemma (d) protruditur, mediante enato ſcapo, in folia, eodem anno quo priora (b) folia, fiet ſpica.

f. Bracteæ in hac ſpica (e) tum ortæ fuere ex foliorum rudimentis uno anno præcocioribus, adeoque teneræ.

g. Dum Bracteas has (f) concipio uti gemmæ (c) ſquamas, in folia enatas (d), ſequitur etiam quod concipiam in eorum alis hærere alias gemmas minores, ſi bulbus permanſiſſet; Sed ultimæ hæ flores evadunt.

h. Corolla adeoque ſe habet uti gemma tertii anni (g), quæ ideoque duobus annis præcocior exiſtit.

i. Si itidem in ipſa corolla, tamquam in bulbi gemma concipio hærere minores bulbos, videbo hos mutatos eſſe in ſtamina; adeoque Stamina quarti anni ſoboles ſint; imo & piſtillum quinti anni.

Qui naturam inſectorum ſcrutati ſunt, invenerunt, quod ſic dicta metamorphoſis in inſectis, proprie non ſit tranſubſtantiatio, qualem *OVIDIUS* ſibi repreſentavit, ſed tantummodo decorticatio: Et *SWAMMERDAM* clare obſervavit, quod in larva Papilionis Braſſicæ, cum etiamnum in terram reptat, alæ & totus Papilio, ſub ipſo cortice abſconditus eſſet; adeo ut hæc metamorphoſis, denudatio partium tantum eſſet, eodem modo ac in floribus. Si jam flores inſpiciamus, videbimus eos nihil aliud,

FIGURE 3. Addition to thesis *Metamorphosis Plantarum* (*in* Linnaeus, 1759c, pp. 331, 332; paragraphs between arrows added in this version).

with parts of the adult insect and the particular tissues from which they arose. He then went on to discuss this metamorphosis in the context of the growth of *Scilla* and *Ornithogalum*. He suggested that a bud in the axil of a leaf might produce additional leaves the following year, or it might develop into a spike in the same year that the leaf was produced. The leaves on the spike—the bracts—were tender because they were precocious, representing the leaves of the next year's growth; like other leaves, they bore buds in their axils, but these developed immediately into flowers. The corolla (perianth) was thus the bud of the third year and developed two years in advance, the stamens were the "shoots" of the fourth year, and the pistil that of the fifth year.

The details of the equivalence of the several parts of the flower with a particular year's growth might differ, as with the version in the *Systema Naturae* just mentioned, but the principle was the same. Linnaeus equated each morphologically different part of the flower (or inflorescence) with one year's growth. Since both *Scilla* and *Ornithogalum* lack bracteoles and have a perianth rather than a readily distinguishable calyx and corolla (see below), the differences in the two versions of prolepsis outlined relate to differences between these monocotyledons and the more common arrangement in dicotyledons. A similar variation of this basic theme is found in Linnaeus's explanation of double

flowers in the Compositae: the involucre represented the "shoots" of year two; the receptacular bracts, those of year three; the pappus, year four; the corolla, year five; and the petaloid pistil, year six (Linnaeus, 1760c).

These two theses on prolepsis thus represent the extended justification and discussion of the mature form of the theory of anticipation. There was a close parallel between the growth of the vegetative branch and that of the flower "wherever leaves are found, there between the substance of the cortex is the fiber of the medulla"; ". . . the cortex produced leaves, thus leaves are nothing other than "shoots" advanced from the cortex and can produce new life" (Linnaeus, 1760c, pp. 4, 11). In the flower, of course, the medulla produced bracts and calyx with cortex, stamens with lignum, and so on; all these structures were basically cortical in origin. Within "the substance of the cortex" (e.g., Linnaeus, 1763, p. 7), which made the floral organs, was to be found the pure medulla in the pistil; in buds, imbricate leaves enclosed the medulla. In both vegetative and floral buds the leaves were associated with buds (but see below). "The tree (*sic*) then produced the flower, nature having anticipated the progeny of five years then producing together [and] forming from budded leaves ("foliis gemmaceis"), bracts, calyx, corolla, stamens, and pistil, and the seed filled up with granular medulla terminating the life of the plant" (Linnaeus, 1767b, p. 9; see also 1763). Note, however, that as with the earlier simpler equation of "tissue" types with different parts of the flower, the parts of the flower involved in prolepsis do not correspond exactly to the seven parts of the fructification that provide the natural characters of genera—calyx, corolla, stamen, pistil, seed, pericarp, and receptacle (see above and TABLE 1). Also, the cortex proper is involved in two years' growth, the other tissues in one.

Linnaeus noted that prolepsis occurred in some animals; in *Volvox globator,* which he included in the Zoophyta (the sixth and last order of the Vermes, in the animal kingdom; see below), he described a comparable series of generations as being visible inside the body of the minute adult (Linnaeus, 1758) and a similar phenomenon was known in species of *Aphis.* Anton van Leeuwenhoek was the first to note what he thought were "seeds" in *Volvox* in 1700 (see Dobell, 1932). Further, the figure five in the five years of the mature theory of anticipation was in line with Linnaeus's favored quinarian numerology (e.g., Jonsell, 1979; Lindroth, 1983; Broberg, 1985).

But there is a tension in Linnaeus's reasoning here, at least to a twentieth-century reader (Guédès, 1969). Linnaeus did not distinguish clearly between axillary and terminal buds but considered that all buds occurred in the axils of leaves of flowering plants; he had no notion of a terminal bud continuing the growth of the stem (see Löfling, 1749). Thus if a flower bud really represented six years' growth, the parts of the flower would come from a series of buds successively borne in the axils of the leaf or leaves of the preceding years' growth, and this is how Linnaeus (e.g., 1760c) discussed that relationship. All the parts of the flower would then be opposite one another. However, Linnaeus (e.g., 1751a, pp. 57, 61) knew that the sepals and petals, at least, alternated in their positions.

There are additional complications caused by attempts to equate each year's growth in vegetative branches with a particular tissue (see FIGURE 2B). Linnaeus

(1763) discussed the detailed structure of the vegetative bud and compared it to that of the flower in the thesis *Prolepsi Plantarum.* The leaves of the first (current), second, and third years came from the cortex, those of the fourth year from the liber, and those of the fifth from the wood. For the leaves of the sixth year, he invoked membranes almost touching the medulla, which he compared to the meninges surrounding the central nervous system of vertebrates. Of course, the sixth year's growth, or the "shoots" of the sixth year, corresponding to the pistil in the flower, could not be the medulla itself, because the medulla was needed to continue the growth of the shoot, whereas in the flower the medulla could be used up in the formation of the pistil, since with flowering the shoot that bore the flower died.

As Linnaeus (*ibid.*, p. 11) went on to say, "Whenever the budded leaves of the first year, which are outside, develop into a branch with its leaves and buds, then as much medulla [as remains] in the axils of the leaves of the sixth year, which are concealed in the intimate shades of the plant, protrudes as the new budlet rudiment (nova protrudit rudimenta gemmulacea) for the seventh year, and thus growth is prolonged" (cf. Guédès, 1969, p. 338; translation of "protrudit" as the ambiguous "produit"). The protrusion of the medulla beyond the cortex agrees with the ideas Linnaeus expressed elsewhere (see above) of the medulla pushing upward and outward and forcing the more rigid cortex apart; continuation of growth is by the medulla in the ultimate (sixth) year's budlet itself budding. Since the mature leaves are always cortical in origin, although this is not always clear in Linnaeus's writings (Guédès, 1969), the development of the vegetative bud described above is at some variance with the normal pattern of tissue development. The inner leaves effectively have to change their nature from wood to liber and then to cortex before they expand, and this direction is the reverse of that in which the tissues develop in the stem.

The Relationship between Plant Parts

With Linnaeus, as with later proponents of the foliar theory of the flower, the analogy between floral and vegetative shoots is connected with that between all appendicular organs. It is not clear which analogy came first to Linnaeus, although the evidence suggests it was the second (see below). Evidence for the equivalence of all lateral organs came largely from the nontaxonomic findings of teratology (note that Sachs (1890) somewhat underrated this aspect of metamorphosis).

A number of interesting abnormal phenomena were early discussed by Linnaeus, although not initially from the point of view of interchangeability of plant parts. Thus in a double flower ("flos luxurians") some parts were multiplied and others destroyed; there might be many petals but few stamens, yet no interconversion between the two was noted (Linnaeus, 1736a). The calyx and corolla sometimes could not be sharply distinguished since in a number of taxa, including *Daphne* and *Ornithogalum,* they formed a single body. This was green and tough on the outside, so showing its calycine quality, and thin and colored on the inside, due to its corolline nature (Linnaeus, 1738, in a discussion of Cesalpino's work; see below). This arrangement is particularly

common in spring-flowering plants, and it was later suggested (Löfling, 1749; see also above) that in such cases the substance of the liber did not draw back or separate from the cortex.

There was abundant evidence for the basic similarity of appendicular organs in the changes and intergradations manifest in the various terata, or growth monstrosities, known to Linnaeus and his contemporaries, information on which was summarized in the thesis *Metamorphosis Plantarum* (Linnaeus, 1755a). Guédès (1969) gave a particularly thorough analysis of this aspect of the "metamorphosis" of plants. These terata included doubled flowers, in which the stamens, and sometimes also the pistils, were changed into petals, resulting in sterility (Linnaeus, 1751a, 1755a). Extreme changes also occurred when whole flowers, series of flowers, or even a leafy branch bearing flowers, were produced from the pistil of a simple flower or the receptacle of an aggregate flower like a scabious or a thistle; this is the phenomenon Linnaeus (1751a) called proliferation. Galls and other kinds of insect infestation provided similar evidence of metamorphoses—*Pistacia* produced long, purple follicles, *Cerastium,* imbricate capitula, and so on (Linnaeus, 1755a). In such terata organs changed their form, and such changes, appropriately interpreted, gave evidence at the same time of the potentiality, nature of, and relationships between organs. Hence, despite the fact that petals were not produced directly from plain cortex, they were interchangeable with—and in some way fundamentally the same as—leaves, which were.

Since the liber and the wood were derived from the cortex, it is perhaps hardly surprising to see that under the appropriate "physiological" condition—excess of sap—they could become plain cortex again (see Guédès, 1969). This leads to the other major line of argumentation bearing on the relationship between plant parts, which can loosely be described as a physiological-balance theory of development. Much nutriment led to the production of leaves, or more leaflike structures, while less nutriment caused flowering, or flowers with less leafiness. This argument was also in evidence early; the opening questions of the thesis *Gemmae Arborum* (Löfling, 1749; see also above) seem to expect a physiological answer, and in the important addendum to the *Philosophia Botanica* entitled "Metamorphosis Vegetabilis" (Linnaeus, 1751a, p. 301, translated in part below; see also Celakovsky, 1885, and Guédès, 1969), the explanation for the rudimentary theory of anticipation advanced two years before by Löfling is expanded in terms of such physiological ideas (it should be remembered that Löfling was acting as amanuensis for Linnaeus during the writing of the book):

> Buds or *budlets* or *flowers* or both are fertile.
> The plumule of the seed is often terminated by a flower or bud.
> The principle of *flowers* and *leaves* is the same.
> The principle of *buds* and *leaves* is the same.
> The bud contains rudiments of leaves.
> *Stipules* are appendices of leaves.
> The *perianth* is made up of connate rudiments of leaves.
> By ("derivato") diverted nutriment to the scales of an ament, the destroyed florets are changed to *Leaves.*
> By nutriment diverted to the florets of an ament, the leaves are made *Calyces.*
> Moderate growth produces flowers from the terminal leaves.

This style of explanation was elaborated over the next 15 years (see especially Linnaeus, 1763). It was a well-established horticultural observation, and several times commented upon by Linnaeus (e.g., 1755a, 1760c, 1762a), that plants in fertile ground were wont to branch profusely and produce lots of leaves but few flowers. When the cortex was well nourished, the medulla could not emerge (Linnaeus, 1759a). In poorer and especially drier conditions this relationship was reversed, with less vegetative growth and more flowering. Similarly, plants (such as species of *Dianthus, Papaver,* and *Anemone*) that produced flowers with numerous petals when grown on good soil bore simpler flowers with fewer petals when grown in poorer ground (e.g., Linnaeus, 1755a, 1760c). With an excess of the descending, vegetative force, either more leaves or more petals resulted (petals, of course, although leaflike, were derived from the liber, not the cortex itself; leaves were directly derived from the cortex). As the vegetative force became weaker, the activity of the ascending, generative force in the medulla became more evident; there was freer movement ("propulsioni") in the medulla, the cortex was weaker, and so the medulla emerged further from the cortex and produced flowers.

The general balance theory extended to taxa like *Lilium bulbiferum* and *Dentaria,* where plants with bulbils did not set seed (e.g., Linnaeus, 1763); vegetative forces were again in excess. The different sexes of flowers could in part be at least similarly explained; in male flowers the medulla found its way through the cortical substances but did not have the force to expand into the pistil, dying off or drying out (Linnaeus, 1763).

There is thus abundant evidence that Linnaeus envisioned the fairly ready transition between the different parts of the flower. (This differed from the situation in animals, where in one ambiguous passage Linnaeus (1760c, p. 19; see also Guédès, 1969) suggested that a liver could not change into a heart, or a heart into a stomach; each had its own nature ("sed singula suum retinent principium").) Nevertheless, although transitions occurred, intermediate structures on normal plants were uncommon; they were varieties, variations from the taxonomic or essential norm that depended on fixed and discrete gaps between both the organs of plants and the taxonomic groups.

The situation was not so clear when the pistil was considered; it was normally medulline, yet in doubled flowers it could become petaloid-cortical. Linnaeus suggested that the pistil was indeed covered by a very thin layer of cortex, and it was this that developed and made the pistil—the "shoots" of the sixth year—on occasion foliaceous. However, when this was the case, there was nothing—i.e., no medulla—present in those "leaves" ("Quod si ulterius pistilli mutationem in folia ostendere foret animus . . ."—Linnaeus, 1760c, p. 18). Medulla and cortex were not interchangeable, yet the largely medullary pistil could still be the leaf of the last year in the proleptic series. This version of the development of the flower is similar to that of the vegetative bud discussed above, with "special" tissue of cortical origin, yet not part of the normal series of tissues of cortical derivation, giving rise to the leaves of the ultimate year.

The Cortex-Medulla Theory and Hybridization

The cortex-medulla theory also played an important role in Linnaeus's ideas on hybridization. In normal reproduction the medulla, the internal structure of the plant, its essence, was effectively continuous through time and successive generations since creation because it remains unchanged in the seed (Linnaeus, 1759a). Or, more accurately, the pistil, derived from the medulla, was unable to lay the foundations for the life of the new plant until the woody essence of the stamen had been absorbed by the medullary humor of the pistil (Löfling, 1749; see also above). Later Linnaeus (1767b; see also 1759a) talked about the copulation of the "cortex externa" with the medulla, the medulla in this case being compared to nerve fibers, producing the new life of the plant. Thus the woody essence from the stamen, representing the cortex, and the medulla, from the pistil, were both represented in the seed.

After 1747 in particular, Linnaeus became much interested in the phenomenon of hybridization, although it took him about ten years to develop his views on this subject (Larson, 1971). Excellent summaries have been provided by Bremekamp (1953), Hagberg (1953), Hofsten (1958), Larson (1968, 1971), Stafleu (1971), and Broberg (1985), while Zirkle (1935) included extensive translations of Linnaeus's writings on hybridization. In hybridization the constancy of species form required for Linnaeus's taxonomic system would appear to break down. There is, however, less conflict when such simple hybridization is explained in terms of the cortex-medulla theory. As Linnaeus saw it, hybridization was like any other fertilization event, with involvement of the stamen, basically cortex, and the pistil, pure medulla. The results were perhaps even predictable. Although the hybrid might resemble the father in overall appearance, "with regard to the inner medullar substance and fructification it is the image of the mother" (Linnaeus, 1771, p. 107; see also 1751c, 1759d, 1760a, 1762b) and was thus more likely to be classified in the same genus as the mother (see also Hull, 1985). In an addition to the thesis *Plantae Hybridae* (Linnaeus, 1756a), the analogy between larvae and the vegetative part of the plant was drawn (see above), implicitly suggesting a comparison between the male contribution and the nonessential covering of the metamorphosing insect. As Hofsten (1958, p. 80) aptly remarked, "the new species were the old ones in new array." They were the old ones because they had the same medulla and were in the same genus; they were in new array because they had a different cortex. There were, however, possible taxonomic problems for Linnaeus when infrageneric hybridization was considered; varieties, and variation in general, might be the result (Linnaeus, 1762b).

Toward the end of his life, Linnaeus developed larger ideas as to how much plant diversity could be explained by hybridization (see particularly Hofsten, 1958; and Larson, 1971). The details of these complex theories need not concern us here, but the basic results of hybridization at any level would be expected to be the apparent physical dominance of the father but the taxonomic dominance of the mother. God created organisms with medulla covered by the

principles of the various kinds of cortex; these were the ordines naturales. Successive hybridizations produced genera, species, and varieties (Linnaeus, 1764; see Bremekamp, 1953, and Larson, 1971, for translations). Bremekamp (1953) calculated that up to 216,000 species could be produced by this whole process—rather more than the 10,000 or so Linnaeus believed existed. During these hybridizations, what was originally undifferentiated medulla is gradually modified by the different cortices that God had created.

Bremekamp (1953) saw this hybridization theory (as in Linnaeus, 1762b, 1764) as justifying the levels of the Linnaean hierarchy. He thus suggested that it not only explained the generation of taxonomic *diversity* in plants, but also the fact that there was a taxonomic *hierarchy.* However, it should not be forgotten that there are five levels of the Linnaean hierarchy—the four just mentioned, as well as the classes into which the ordines naturales were grouped. Also, there were suggestions that hybridization provided Linnaeus with a reason why his families (ordines naturales) could not be defined. Problems surrounding the definition of such families were not simply caused by the tension between the recognition of such families by their habit and their definition in terms of fructification characters. Hybridization might even lead to the recombination of these fructification characters, which would mean that they would not be restricted to any particular family (Malmeström & Uggla, 1957; cf. Larson, 1971; see also above). But hybridization between species or even genera would not necessarily disturb the economy of nature (Atran, 1990; see also below); the properties of congeneric plants are largely the same and are unaffected by hybridization (Linnaeus, 1762b). Finally, if all possible hybrid combinations are produced, the "form" that taxonomic diversity takes is likely to be very regular, and depending on the nature of the interactions of cortex with medulla, without any particular gaps (Eriksson, 1983), a subject to which we now turn.

Continuity and the Cortex-Medulla Theory

Linnaeus, although believing both species and genera to be discrete, considered that at higher taxonomic levels there were no particular gaps.[10] Linnaeus's great interest in the *peloria* variant of *Antirrhinum* (see the thesis *De Peloria,* defended by Rudberg; Linnaeus, 1744) shows his concern over change that transgressed established boundaries. *Peloria* was an example: how could a genus arise *de novo,* since genera were immutable and discrete? But *Peloria* could be fitted into his general taxonomic scheme of discrete, generic-level entities. Additionally, in *De Peloria* the intermediate nature of corals, Abraham Trembley's work on polyps, and the production of wingless aphids by winged aphids also received attention. All these phenomena were later integrated with his ideas of systematic continuity at higher taxonomic levels, although it was perhaps not so much the change from winged to wingless in aphids that was emphasized by the later Linnaeus, but the way in which they reproduced.

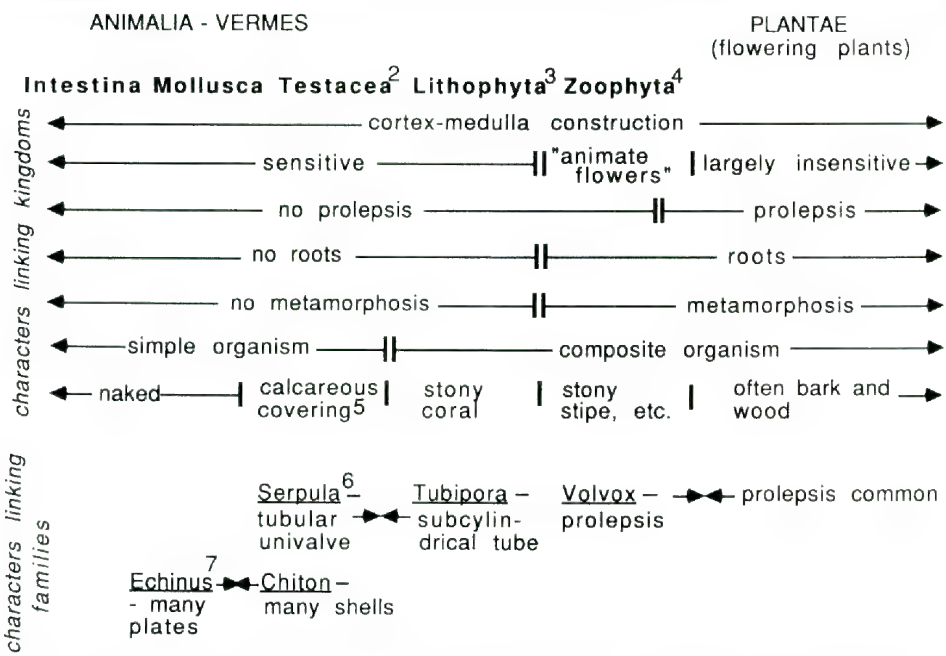
[10]Broberg (1985) rightly noted that although Linnaeus crossed out "natura non fecit saltus" in his own copy of the *Philosophia Botanica,* this was simply an editorial correction; the phrase was repeated twice in the same section, and Linnaeus allowed the second mention to stand.

The comparison of the vegetative bud with a polyp, and of seeds with an egg-bearing animal (e.g., Linnaeus, 1749), was important in heralding the integration of the cortex-medulla theory with ideas of continuity (for a good treatment of this, see Broberg, 1985). Practically all the different aspects of the theory were involved. The thesis *Animalia Composita* (Linnaeus, 1759a) presented the justification for Linnaeus's remodeling of the arrangement adopted in the last part of the animal kingdom in the tenth edition of the *Systema Naturae* (Linnaeus, 1758), a rearrangement that can be understood only in the context of the cortex-medulla theory. As noted above, Linnaeus frequently compared the medulla to part or all of the nervous system of animals, and in the thesis *Animalia Composita,* for example, animals were said to have the same general cortex-medulla construction as plants (see also Linnaeus, 1759d; Lindroth, 1983; Broberg, 1985). The medulla of plants was equivalent to the spinal medulla of animals, that is, to the spinal cord itself. Thus all organisms possessed the cortex-medulla type of construction. However, the constraint exercised on the medulla spelled one of the differences between most animals and plants. The latter were composite organisms because the medulla was able to push through the cortex and form buds; in animals, the medulla remained strictly enclosed by cortex, so buds could not form and the organism remained simple. Plants were branched, and this branching was the manifestation of the inherent multiplicative property of the medulla (see below). But in worms and some other animals, there was also no constraint to the medulla, no hard vertebral column, and so the medulla could escape in the same way as it did in plants (Linnaeus, 1759a). Thus a single articulation of *Taenia* had life, just as a single articulation of the root (rhizome) of *Triticum repens* could give rise to a complete new plant (Linnaeus, 1767a). Composite animals were placed next to flowering plants in Linnaeus's scheme of things (see TABLE 2).

In TABLE 2, the distribution of this feature along with others that come from plant and animal construction are superposed on Linnaeus's grouping of the Vermes (see Linnaeus, 1758). The class Vermes ended with three orders. The first, the Testacea, were bivalve and gastropod mollusks in which a single animal was covered by a hard shell. The next group, the Lithophyta, were "composite molluscan animals, sprouting out from strong underlying coral in which they are grafted and which they build" (*ibid.,* p. 789). A shell is there, but in this group the animals are "composite," being organically connected. Linnaeus described the animals involved as nereids, which he would probably have put in the order Intestina if they had not been enclosed in stony matrix, or as hydroids, which he would likely have placed in his last order, the newly circumscribed Zoophyta, if they had been free living (see Linnaeus, 1745, for earlier arguments as to whether corals were plants, animals, or stones, and if animals, whether they were to be classified by the coverings or the organisms contained). The Zoophyta consisted of "composite flowering animals with an animated body (stirps vegetans)" (*ibid.,* p. 799), one of its members, *Hydra,* being described as a sensitive flower (note that the Zoophyta were originally placed with plants—e.g., Linnaeus, 1737).

These three orders, particularly the Zoophyta, were all more or less anomalous in the context of typically animalian features. The Zoophyta in particular

TABLE 2. **The Linnaean scala at the juncture of animals and plants.**[1]



[1]This table depicts the distribution of different features "separating" animals and plants. Most of them also occur in some, but not all, members of the Animalia-Vermes and sometimes isolated elsewhere as well—for example, prolepsis in *Aphis* (Animalia-Insecta-Hemiptera). The vertical lines give some indication of the degree of separation between the groups afforded by each feature. Also shown are some bridging genera that blur the lines of separation between families, making smaller-scale linkages.

[2]The animals inhabiting the shells of the Testacea are usually referred to molluscan genera, but *Teredo* belongs to the Intestina (see also Linnaeus, 1771b, for problems in classifying shells; and Lindroth, 1983, for references).

[3]The animals inhabiting the Lithophyta belong either to the Mollusca (*Nereis*) or the Zoophyta (*Hydra*).

[4]The "flowers" of the Zoophyta are usually referred to *Hydra*, itself a zoophyte, rarely to *Medusa*, a mollusk.

[5]Details of the various stony and woody coverings differ, but the fact that these groups all have coverings of one sort or another is important.

[6]*Serpula*, the last genus in the Testacea, is the only one in which the animal is described as being a *Teredo*; this may be in part because of the similarity of a *Serpula* "shell" to the calcareous lining of an exposed burrow of *Teredo*. *Serpula* in Linnaeus's sense contains wormlike annelids that, if free living, would probably have been placed by Linnaeus in his Intestina. *Serpula penis*, however, is a lamellibranch mollusk; paired shells can be seen at the end of the tube (K. Boss, R. Turner, pers. comm.). The genus adjacent to *Serpula*, *Dentalium*, has a tubular shell and is included in its entirety in the Mollusca today (see also Dodge, 1952, for the taxa included in the Testacea; Winsor, 1976, for a description of serial sequences in Linnaeus's insect classification.

[7]Linnaeus did not mention the distinctive, rather platelike construction of many echinoid coverings here, but these are very evident. The general arrangement of the Testacea is: first, genera in which the shells have many valves, then genera with two valves, then genera with one spiral valve, and finally genera with one valve that is without a regular spiral (see also Cain, 1983).

were constructed like plants, yet they were more obviously like animals in their behavior. They often had roots; they were generally caulescent, with life multiplying in branches; they had buds that could be removed; and they metamorphosed into an animate flower that had the power of voluntary movement and that itself changed into seed-bearing capsules (Linnaeus, 1758, p. 643). Although the Zoophytes lacked leaves, Linnaeus (e.g., 1751b) suggested that the leaves of a plant might indeed be organs of motion that were passively moved by the wind. The articulations of the Zoophytes were the "exuviae" of the animal, solid cortical tissue, the result of a process similar to that by which the cortex of the bark changed into solid wood (Linnaeus, 1759a). Linnaeus noted that the Zoophyte *Hydra* behaved like *Salix* in that its separated buds could grow into independent organisms;[11] the ability of *Salix* cuttings to grow so readily provided him with a good example of the role of the medulla in vegetative growth, just as its catkins provided an early example of prolepsis. The last genus in the Zoophyta, *Volvox,* included *V. globator,* which as we have already noted showed yet another plantlike feature, prolepsis. To summarize, the species placed in the Zoophyta and Lithophyta were complex organisms in which the notion of individuality developed for higher animals was inappropriate, but which were more plantlike in this respect as well. The Zoophyta even included *Taenia,* the tapeworm, which had earlier been classified in the Vermes-Reptilia (Linnaeus, 1756; of the Vermes-Intestina of Linnaeus, 1758), but which Linnaeus came to believe was also a composite organism, the articulations of which had internal flowers!

TABLE 2 shows clearly the nature of Linnaean continuity with an overlapping, catenalike distribution of characters, all of which come from Linnaeus's understanding of the cortex-medulla theory; we can find no other relevant characters. It is interesting that both Linnaeus (e.g., 1759a, p. 4) and Fabricius (*in* Giseke, 1792, pp. [2], 4) used the word "catena" in the same context of continuity. Plantlike features are found in many animals, so making the distinction between the two somewhat a matter of taste. As can also be seen from this table, features of plants do not simply overlap into animals, being found throughout major taxonomic groups. They may occur in only a *part* of these groups—a part that Linnaeus placed immediately adjacent to groups in which these features were constant. In a world in which continuity rules, "groups" are circumscribed by more or less arbitrarily selected characters and cannot be defined by covarying characters (see also Lamarck, 1778).

Note that in the Testacea and Lithophyta, Linnaeus gave the general identity of the organism inhabiting the hard covering the particular nature of which defined these groups—e.g., "Animalia Teredo." In the Zoophyta there are comparable references to these organisms, but as flowers: for example, "Flores

[11]Abraham Trembley's then recent, but already celebrated, work on *Hydra* paid great attention to its capacity to grow and regenerate (e.g., Trembley, 1744). Dawson (1987) discussed Trembley's work in some detail and showed that some of his experiments were performed because of his beliefs that *Hydra* was a plant and that plants were inside-out (not upside-down) animals. Dawson also detailed the impact of Trembley's work on Charles Bonnet, who, unlike Trembley, interpreted this and other evidence as support for the existence of a Ladder of Natural Beings. Bonnet's (1745) arrangement of continuity along this ladder differs in detail from that of Linnaeus.

Medusae" and "Flores Hydrae." It is interesting to see that the actual metamorphosis represented by the appearance of those flowers was interpreted as being more like that of plants than that of insects, since the zoophyte flower did not separate from its stalk, unlike the imago of the insect (Linnaeus, 1762b). From the Zoophyta with their "flowers" and largely vegetable (flowering-plant) type of construction, it was of course a short step to the flowering plants, the next group in the scheme of things. It should be remembered, however, that Linnaeus (e.g., 1766a) considered the Zoophyta to be the link among all *three* kingdoms, the mineral kingdom included.

Unfortunately, it is impossible to follow the linkages within flowering plants by studying the arrangement of plants in the *Genera Plantarum* or the *Species Plantarum,* since both followed the sexual system that did not represent natural relationships as Linnaeus saw them. The fragments of a natural arrangement that Linnaeus (e.g., 1738, 1751a) produced lack the characterization of the groups recognized that might allow the kind of analysis presented here to be taken further. However, the partially characterized groups in Giseke (1792) may be susceptible to such an analysis, although the form that the continuity is likely to take will probably not be linear, as the illustration of the relationships of these groups (*ibid.,* figure facing p. [623]) suggests. Of course, any "combinatorial" hybridization of cortex and medulla (see above) is also unlikely to generate linear continuity. Although Linnaeus grouped genera into natural families, from Giseke's figures it is clear that some genera bridged gaps between groups; there were also plants not yet discovered that might fill the gaps. In addition, a property of "natural" groups in a world of continuity needs emphasizing here. Such groups contain a portion of the real (continuous) order yet are artificial in that their boundaries are not evident in nature. That our groups have more or less "real" boundaries should not blind us to the distinctive nature of Linnaean higher taxa (as well as those of Lamarck and De Jussieu).

VOLVOX CHAOS, CHAOS PROTHEUS, AND UNRESTRAINED MEDULLA

The last species mentioned in the first volume of the tenth edition of the *Systema Naturae* (Linnaeus, 1758) is *Volvox chaos,* which Linnaeus found to lack definite form, in this respect being "more inconstant than Prometheus (*sic*)" (*ibid.,* p. 821). In the twelfth edition of the *Systema Naturae,* Linnaeus (1767b) again remodeled the last part of the Zoophyta, and he added the genera *Furia* and *Chaos,* the latter including *Chaos protheus* (*sic*), the erstwhile *Volvox chaos,* and other minute organisms. (The word "chaos" has several connotations: Chaos was a primordial world of disorder, formlessness, and confusion; Linnaeus's genus *Chaos* was certainly all three.)

Linnaeus (1767a) included details of recent discoveries of submicroscopic life in the thesis *Mundum Invisibilem.* He discussed Otto von Münchhausen's work on fungi both extensively and with approval. Von Münchhausen had claimed to have found animalcules developing from the seeds of such fungi as *Ustilago, Lycoperdum,* and *Agaricus,* so perhaps making fungi animal, rather than plant, in nature.[12] Linnaeus (1767a) speculated that fungi might better be put in a new kingdom, perhaps along with polyps and infusoria ("Moleculae vivae"). He (1767b) placed the animalcules coming from fungi in the genus

Chaos (as *C. fungorum* and *C. ustilago*), *Chaos* being the genus that contained infusoria and animalcules of all sorts. Linnaeus even thought some diseases were perhaps caused by organisms that should be placed in this genus. To Ramsbottom (1941, p. 297) this recognition of the genus *Chaos* represented a "lamentable lapse" on Linnaeus's part: "So acute in his sense of affinities, so sure footed in so many different fields, Linnaeus here came sadly to grief." But Münchhausen's findings must first be interpreted from Linnaeus's point of view (for other literature on Münchhausen, see Ramsbottom, 1941; Ainsworth, 1976; Broberg, 1985). *Chaos* itself fitted readily into the general superstructure of the cortex-medulla theory.

This new kingdom to which Linnaeus alluded was intermediate between the animal and plant kingdoms ("neutrum seu chaoticum vocetur"—Linnaeus, 1767a, p. 12). It was, however, not so much in disorder as made up of organisms lacking precise form. Thus the last scholium in the thesis addressed the issue of whether these smallest animals were pure medulla, lacking an organic body. Pure medulla might be the seat of life, yet it was formless, or at least without constant form; only when constrained by and interacting with the cortex was definite form generated.

In addition, that Münchhausen's fungi should develop into microscopic worms would surely find ready resonance in Linnaeus since he had earlier (1751a) noted that the fungi were in classificatory chaos, with specific and varietal limits being indistinct because of the lack of constant form in these organisms. Perhaps the problem with fungi was that they lacked much hard cortex; to Giseke (1792), probably reflecting Linnaeus's later thoughts on the subject, this lack certainly explained how fast fungi grew (here Giseke is apparently reporting on his studies with Linnaeus in 1771). The variability of fungi, the greatest of any plant, again occasioned comment. It was almost to be expected that classification, which depended on constant morphology (this in turn depending on the interactions of rigid cortex and medulla), would be so difficult in the fungi.

Animation was the major characteristic of life, a characteristic that resided in the medulla. Linnaeus (1767a, p. 19; see also above) even considered the possibility that the medulla of the inanimate plant itself might be animated, although being constrained by the cortex it could not show this property. Small wonder that when organisms were made up of pure medulla they showed active movement and sensitivity, but not constant form.

Linnaeus toyed with the idea that the relationship between the plant and animal kingdoms was similar to the metamorphosis that occurred in the development of plants and insects, that of the plant in particular occurring during prolepsis and the shedding of its covering ("ut viderentur ipsa naturae adyta penetrari detegendo *prolepsin* transformatum per antipraegnationem"—Linnaeus, 1767a, p. 20). Zoophytes also showed this metamorphosis, but becoming

[12]In the eighteenth century, fungi growing out of insects or other animals were discovered. Linnaeus (1753) initially included these fungi in *Clavaria*, but species like *C. militaris* were eventually transferred to *Cordyceps*. Although there was considerable debate as to whether or not such "vegetable flies" or "vegetable wasps and plant worms" (Cooke, 1892) provided evidence of heterogenesis, they do not seem to have played an important role in that element of Linnaeus's thinking under discussion here (see Lütjeharms, 1936; Ramsbottom, 1941).

more like animals in the process ("per metamorphosin abire in animalia, quemadmodum plantae in flores" (*ibid.*)); hence, plants could possibly metamorphose into animals—witness Münchhausen's findings. So prolepsis, metamorphosis, and the cortex-medulla theory were adequate to the challenge presented by this unexpected microscopic world, although clearly an even larger issue is raised—that of the nature of the generation of life itself (Broberg, 1985). Preformation was, however, clearly not involved (see also Farley, 1982, but cf. Goethe, 1891, p. 322).

Goethe, De Candolle, and Metamorphosis

Goethe developed his ideas on the relationship between the appendicular organs of plants in his *Versuch die Metamorphose der Pflanzen zu Erklären* (Goethe, 1790; additional references are to the translation by Arber, 1946) during his travels in Italy, and especially in Sicily in early 1786.

On the surface there is general congruence between Linnaeus's and Goethe's views on plant form, both involving a fundamental similarity between organs of the plant that appeared at first sight distinct. Goethe emphasized annual plants (Arber, 1946), while Linnaeus stressed perennials and trees, although as we have seen, the latter did not entirely ignore annuals (to Goethe, Linnaeus's ideas seemed to mean that annuals were plants originally destined by nature to live for six years). In his almost exclusive consideration of the above-ground, appendicular parts of the plant, Goethe effectively deemphasized Linnaeus's downward, vegetative movement, being little concerned with the root, but so was Linnaeus in his morphological writings. Goethe considered that the generative tissue of the plant was the liber, not the medulla, and that the various parts of the flower represented a series of expansions and contractions of tissue under the influence of an ever-more-refined sap. He saw all seven appendicular parts of the plant (leaves, calyx, corolla, stamens, style, fruit, and seed) as representing six steps, three successive expansions and contractions: stem leaves (expansion) and calyx (contraction), petals (expansion) and sexual organs (contraction), and fruit (great expansion) and seed (great contraction). This idea of the development of the plant is more complete than that in most versions of Linnaeus's theory of prolepsis (but cf. Linnaeus, 1746), all parts of the plant being involved; Goethe also did not discuss particular tissues not being responsible for producing particular organs. Goethe emphasized the interchangeability of floral and vegetative organs, citing evidence very similar to that given by Linnaeus and placing great weight on teratologies like doubled flowers and on transitional organs. For Goethe, the group of structures that Linnaeus called nectaries played an important role both in the progressive refinement of the sap of the flower, refined sap being needed for the production of the sexual organs, and in demonstrating intermediacy in form between the petals and the stamens.[13]

[13]Interestingly, others found Linnaeus's term "nectary," which he used in a taxonomic context but with an almost physiological definition (e.g., Linnaeus, 1751a), to be unsatisfactory for their largely taxonomic concerns. Linnaeus (1762a) listed 18 different kinds of nectaries in addition to other glandular structures outside the flowers; all secreted nectar, or apparently did. However, his contemporaries and their immediate successors thought that there should not be a single term, "nectary," since these structures were very different in nature (see, for example, Turpin, 1815; Stevens, 1984a).

The main difference between Goethe and Linnaeus is less in the detail of their explanations of how tissue and form were generated, although there are substantial differences, and more in the role these ideas played in their thought. The two belonged to entirely different intellectual generations. At the risk of oversimplification (see below), it can be said that Linnaeus ultimately needed constant and discrete characters to be able to classify, and his theories on metamorphosis, prolepsis, and hybridization involve a fairly precise and circumscribed causality of form. Goethe, on the other hand, adopted a more Neoplatonic approach, seeing unity in nature, indeed in life as a whole, and was looking for ideas behind (or in front of) manifest form, more real than the form itself. That form might intergrade was not worrying but the reverse. Goethe (1891, 1901) himself considered Linnaeus's approach limited.

There was a further connection between the two men. When Goethe developed his ideas in 1786, he had with him an old edition of the *Genera Plantarum* (Goethe, 1890; probably ed. 4, published in 1752). He had also apparently read the *Philosophia Botanica* (Mueller, 1952), in which, as we have seen, Linnaeus's ideas on metamorphosis were clearly, if concisely, expressed. Goethe of course made repeated reference to Linnaeus when he later wrote the *Versuch die Metamorphose der Pflanzen zu Erklären.* Ideas of metamorphosis are generally evident in Linnaeus's work from the 1750's onward. Goethe's actual discovery of the idea of metamorphosis was, according to his own accounts (e.g., Mueller, 1952), independent.

De Candolle (e.g., 1827, Vol. 1; see also Guédès, 1972), who also developed the notion of the fundamental similarity of all the appendicular parts of the plant, did so largely independently of both Goethe and Linnaeus; he could not even read German. His ideas are best expressed in his *Théorie Élémentaire* (1813) and especially in the *Organographie Végétale* (1827). In the former the evidence for this similarity came from the intermediacy of form of different organs and the relationship between parts in "normal" flowers, but in the latter he made more of evidence from teratology and also noted briefly the effects of cultivation and the amount of sap on whether or not a plant would flower. He was early (e.g., 1807) interested in the doubling of flowers. He incorporated some of Goethe's terminology into his work but apparently largely ignored Linnaeus. This was perhaps because it had long been evident to De Candolle that Linnaeus's notion that the pistil was made up of pith could not be true of the monocotyledons (De Candolle's "Endogens"). De Candolle (*in* Lamarck & De Candolle, 1805) and others considered that the monocotyledons had no pith. (Compare Lamarck, 1778—he considered pith to be essential for life, its death with age causing the death of the individual.) Although he largely used the same kind of evidence for establishing the similarity of appendicular parts of the plant as did Linnaeus, he did not cite Linnaeus; the approach of Grew and Malpighi was clearly more congenial to him.

De Candolle was perhaps primarily a taxonomist; his morphological work helped his taxonomic studies in that it made the often variable and deceptively simple structure of the flower more comprehensible and regular to him and helped in the development of his ideas of floral "symmetry" (not the same as "type"—Stevens, 1984a). De Candolle's emphasis on the similarity of sepals, petals, leaves, and the like was immediately seen by his contemporaries as

being of great importance, and it was singled out for attention in several of his obituaries (e.g., Dunal, 1842; Brongniart, 1846). De Candolle's work initially stimulated a rather typological approach to floral organization in people like Michel Dunal, Christian Moquin-Tandon, and Auguste de Sainte-Hilaire. Since, however, the limits of plant groups remained vague, the typological approach did not flourish in systematics (Stevens, 1984b).

Linnaeus and Antecedents to the Cortex-Medulla Doctrine

Some of Linnaeus's predecessors had ideas that are—or might be—supposed to have had some influence on the cortex-medulla theory (see also Guédès, 1969). We discuss briefly some aspects of the work of Cesalpino, Mariotte, Grew, Malpighi, and Vaillant, so as to understand more clearly the background to Linnaeus's work.

Andrea Cesalpino, the noted Italian systematist, was considered by Linnaeus (1751a) to be the first, and one of the greatest, "true botanists" and was freely acknowledged (Linnaeus, 1738, 1749) to be the immediate source of the cortex-medulla theory. There is no detailed treatment of his work, although Greene (1983, and references therein) provided an entry into the literature. Cesalpino was a noted Aristotelian scholar, his book *Quaestionum Peripateticarum Libri V* (which we have not seen) being of importance in this context. Characters of the fructification, and particularly those of the seed, were most important in classification for Cesalpino because the multitude of parts they provided allowed distinctions between groups to be made (Cesalpino, 1583; see also Morton, 1981). But they were, of course, also very important functionally, being involved in that vital aspect of the plant's life, reproduction; they were vegetative substance allowing the plant to reproduce (Cesalpino, 1583).

The cortex-medulla distinction and the role of those two parts in the life of the plant pervade many of the introductory chapters of book 1 of Cesalpino's work, but as Sachs (1890) correctly observed, the relation between plant organs and these tissues is different from that usually described by Linnaeus (but cf. Linnaeus, 1747). Leaves in general were indeed produced from the cortex. Thus Cesalpino suggested that deciduous leaves were produced from the outer cortex, evergreen leaves from the inner cortex (liber: Cesalpino, 1583). The calyx and corolla, both on occasion called leaves (folium), were also of cortical origin, but the stamens (flocci) were not mentioned in this context. They were small, and their importance for reproduction was then unknown. It is in the discussion of the origins of the different parts of the fruit that the cortex-medulla distinction is most focused. The fruit arose from the inside of the plant and was made up of three tissues, medulla, lignum, and cortex, which in turn formed the seed and the woody ("cortex") and fleshy ("pericarp") parts of the fruit (*ibid.*, p. 18). The fruit developed after the flower, the stigma plus style ("stamen") of the former being the young fruit (*ibid.*, pp. 14, 19; see also Sachs, 1890).

The position of the medulla provided further evidence of its nature and significance, there being the overwhelming power of the analogy that Cesalpino (1583, p. 3; translated in Sachs, 1890, p. 46) drew at some length between the vital parts of animals and plants. Nature always concealed the principles of

life ("vitalia principia") in the innermost parts, such as the viscera in animals. Hence in plants the principle ("principium") was to be found not within the cortex, but more internally—that is, in the internal medulla—of which much was in the stem but not in the root. The heart or soul of the plant, the "cor," was the junction of the root and the stem but extended throughout the plant. As Cesalpino (1583) noted, the leaves and fruits followed the nature of the cortex, the internal seeds that of the medulla.

Cesalpino's ideas on the parts of plants, their origins, development, and relationships need a more extended treatment than can be given here. However, it may be noted that catkins provided him with a challenge; he thought that in such structures flowers had changed into a different substance—more specifically, that the amentum was produced from the seat of the flower, with the "stamina" (pistils) forming the ament and the petals and sepals ("folia") and stamens degenerating into scales (Cesalpino, 1583; Sachs, 1890). Other flowers were also distinctive in the context of this discussion. Cesalpino surmised that in *Ornithogalum* and *Helleborus* the calyx and corolla were joined, since the leafy organs surrounding the flower were green on the outside and colored on the inside. The flowers of *Cucurbita* and *Punica* presented a different problem: here the calyx was continuous with the outer cortex of the fruit, the flower originating from the fruit ("flos in radice fructus exoritus"—Cesalpino, 1583, p. 16; Greene, 1983, p. 820). Cesalpino also noted the rarity of plants in which flowers were borne directly on branches with thick bark and the progressive purification of the sap of the plant in the flower.

In none of the other works mentioned below (or in Guédès, 1969) does the cortex-medulla distinction assume such prominence. Nehemiah Grew (collected in his *Anatomy of Plants,* 1682; see also Arber, 1941, and Morton, 1981) indeed noted that there were only two parts of the plant that were fundamentally ("essentially") distinct: the pithy part and the ligneous part, "or such others as are analogous to either of these" (Grew, 1682, "Philosophical History," p. 19). However, in his discussion of the anatomy of different plant organs, including seed and fruit, Grew emphasized not "pith" and "wood" but the particular nature of the tissues making up these parts. Although the several tissues of the plant were compounds of these two parts (Grew, 1682, "Anatomy") there were other interesting levels of analysis.

However, the pith was very important because sap moved through it in large part, and the energy and nutritive quality of the sap determined the particular part of the plant that developed; in general, there was progressive purification of the sap as it moved through the plant (Grew, 1682, "Anatomy"). The flower promoted the ascent of the sap, so if there was no flower, the fruit would die. If the flowers were large, much sap would be present, but it would be used up by the flower "like a greedy Nurse, that prepares the Meat for her Child, and then eats it up herself" (Grew, 1682, "Anatomy," p. 37). The intrinsic rate of ascent of the sap of a species was also important; grapes, with rapidly ascending sap, had almost no flower since no increase in sap that the flower could provide was needed.

This is not so different from either the physiological-balance theory of development that Linnaeus propounded, or the ideas put forward by Edme Mariotte

(1679), although Sachs (1890) attributed to Mariotte in particular Linnaeus's idea that the medulla grows by extending itself and its envelopes in a form of intussusception; the pressure of the sap makes the parts of the plant expand. Mariotte (1679, pp. 54, 55) noted that in cuttings the pith ("mouelle") imbibes water like a sponge "and transmits it in the little fibers between the bark and the wood, from where it is pushed in part towards the end of the base to produce roots at the extremity of the little point, . . . and in part to the nodes which are in the air, to make the buds there swell up, and to make them extend in branches and leaves." In his extended analogy between plant and animal nutrition, Mariotte conceived of the former as progressive purification of the sap after initial "digestion" by the root.

Guédès (1969) discussed at length the several indications Grew gave that he recognized an equivalence among cotyledons, leaves, and even calyx and corolla. Such equivalence was widely noted. Marcello Malpighi (1686), who with Grew is considered to be a founder of plant anatomy, discussed such transitions extensively (see also Mobius, 1901; Arber, 1941; Guédès, 1969). Sebastian Vaillant, in his important *Sermo de Structura Florum* (1718) (see Stearn, 1957; Larson, 1971; Stafleu, 1971) dealt largely with sexual reproduction in plants. However, when discussing the transition of stamens and carpels into petals in doubled flowers, he adopted a style of explanation very similar to Grew's (see also Guédès, 1969).

Enough has been said to discern the relationship between Linnaeus and earlier authors in the context of the cortex-medulla theory. The general outline of this theory as found in Linnaeus is evident in Cesalpino (1583), although some details differ substantially. Cesalpino's emphasis was on the fruit and seed, the functions of the flower being poorly understood in his time (see Greene, 1983). Linnaeus, stimulated especially by the discovery of the sexual functions of the different parts of the flower, focused more on the flower. Cesalpino emphasized the importance of the internal structure of the organism as the place where the principles of life resided, hence Linnaeus's (1738) early suggestion that the flower represented the insides of the plant exposed by the tearing of the cortex. By and large, similar flowers presented problems to both Cesalpino and Linnaeus—*Ornithogalum* and catkin-bearing plants figure prominently in the work of both. Embryonic ideas of the transformation, metamorphosis, or general equivalence of plant parts were widespread, being evident in the works of Grew, Malpighi, Vaillant, and other authors (see Arber, 1946; Guédès, 1969).

The expansive power of the sap is alluded to in Mariotte's work, while the constrictive effect of thick outer cortex on the development of flowers and fruits was suggested by Cesalpino. The general idea of plant nutrition in the seventeenth and early eighteenth centuries, exemplified in the work of Mariotte and Grew in particular, is that of progressive purification of the sap coming from the roots, but there was known to be movement of fluid in the other direction as well. The development of particular plant structures was generally considered to be dependent on the presence of the right kind or amount of sap.

Cesalpino himself developed the cortex-medulla theory from a rather tentative analyses of the plant advanced by Theophrastus (for details, see also Greene, 1983). Theophrastus distinguished between core and bark, with wood

occupying a somewhat ambivalent position—perhaps a part of the bark or a tissue coordinate with it. This is the third level of organization; these tissues are in turn made up of varying amounts of flesh, fibers, and sap, while moisture and warmth are the fundamental properties of the plant body (the formal structure of Grew's idea of the plant is similar to this). The composition of plant organs is discussed (Theophrastus, 1916) in terms of the tissues making up the second level of organization. In line with arguments later advanced by Linnaeus and others, Theophrastus (1976) noted that the distribution of food in the tree affected fruiting, excessive food to the vegetative growth being prejudicial to the fruit and leading to a failure to bear.

DISCUSSION

Linnaeus's classically inspired idea that in the flower the inner structure of the plant, its *real* structure, becomes evident to the human eye is central to an understanding of his botanical thought in particular, but to much else besides. The medulla, the form-generating part of the plant, entered most completely into the formation of the pistil and seed and was surrounded by structures representing the different parts of the cortex. The cortex, especially in its vegetative aspect, was largely disposable from the point of view of the adult plant, and this, when joined with his views on plant sexuality, justified the emphasis on the characters of the fructification in the formation of natural genera (e.g., Linnaeus, 1751a). The cortex-medulla theory is also intimately involved in the notion of both prolepsis and metamorphosis, and to a considerable extent in the broad outlines of his arrangement and understanding of living beings, especially of plants and "plantlike" animals.

Clearly, Linnaeus's development of this idea in plants was also influenced by discoveries about *Hydra, Volvox,* the "individuality" of each segment of the tapeworm, and so on, as extensively detailed by Broberg (1985), but Broberg's thesis (p. 167) that "zoology rather than botany steered Linné's mental activity" is perhaps a little overstated. To him (p. 162), "The reproduction observed for the polyp had to affect the conception of reproduction in the main, and it is necessary to consider Linné's very personal marrow-bark [medulla-cortex] doctrine in light of what the polyp-tapeworm had enlightened him about; less so as a result of his botany." In a somewhat similar vein, Larson (1971, p. 106) noted that "Linné had taken note of this theory [the cortex-medulla theory] as early as 1738, but he only found a use for it fifteen years later" in his ideas about hybridization. In the thesis *Taenia* (Linnaeus, 1748) the animal body is indeed discussed in much the same style, although with a terminology rather different from that Linnaeus adopted very soon afterward for plants. However, the cortex-medulla theory is evident in his earliest work. The classical flower became integrated into a new, all-encompassing vision, but the general background to this was accessible to even the young Linnaeus. The assertion that there was a fundamental similarity among all the appendicular parts of the plant, whether via metamorphosis or anticipation, is the culmination of this vision.

In particular, the theory of prolepsis, or anticipation, seems itself not to have

been anticipated in any detail in earlier literature. Linnaeus considered his ideas on prolepsis to be very important (he wrote concerning prolepsis in one of his autobiographical fragments, "Nobody has penetrated further into the secrets of the creation" (Pulteney, 1805, p. 558)); the mysteries of Nature were revealing themselves to him. Linnaeus (1760c, pp. 1, 2; see also Linnaeus, 1763) strongly asserted that his ideas were new:

> Nobody will readily have doubted that the nature of the plant is much simpler than that of animals to such a degree that it is not surprising if in the latter it is difficult to penetrate into the inner recesses of the science. Malpighi and Grew themselves attempted to prepare the way using anatomy, Hales and others by physiology. In truth I have advanced by a third way proposed by me, the lead to be followed in section 10, p. 826, in the Systema Naturae [ed. 10, 1759b, in part translated above], so that others who are unaccustomed to it can follow it without a mistake.

This is by way of introduction to the thesis *Prolepsis Plantarum,* in which he developed the parallel between the growth of the flower and that of the vegetative shoot. Of course, Linnaeus was in general not one to hide his light under a bushel; he also thought that his fragments of a natural method were a masterpiece, and that much else he had done was of similar importance (Malmeström & Uggla, 1957; Larson, 1971; Lindroth, 1983).

Here, perhaps, is a clarification of his apparently hasty dismissal of anatomists as mere likers of botany—botanophiles—whose work did not pertain to the science of botany (Linnaeus, 1736b, 1751a). Stephen Hales, Johann Gesner, and Christian Theophilus Ludwig, all interested in the "laws" of botany, the anatomists Grew and Malpighi, and the physiologist Bernhard Feldman were all included in this sorry group. Their discoveries, whether in anatomy or physiology, did not pertain to an understanding of that aspect of plants by which their essence was revealed and their form in general made manifest. Those physiologists who were included among the "philosophers" of botany—Thomas Millington, Joachim Camerarius, Vaillant, and Johann Gustav Wahlbom—were mentioned because their work contributed to an understanding of plant sexuality. This was of much more central importance to Linnaeus's thought than findings on cell structure, and he credited Millington and colleagues with having revealed the laws of nature and the mystery of sex. Earlier, Linnaeus (e.g., 1741) had characterized the work of the botanophiles by its lack of interest in the fundamentals of botany; that is, it was not involved in the disposition of plants (into species, genera, orders, classes), or in their naming.

It may also be noted that Linnaeus (1751a) observed, albeit with some reluctance, that the use of a lens was not essential to an understanding of his sexual system, despite some people's protestations. Microscopes were, however, essential in anatomical work, even if an anatomist like Grew deliberately started out by recording what the unaided eye could see, only after that using a lens. Interestingly, Linnaeus seems to have been dissuaded by Albinus (probably Bernard Sigefred Albinus; see Mirbel, 1810) from following up on an initial wish to study anatomy. Anatomy and taxonomy did not begin to be integrated in botany until the late nineteenth century.

The ideas of prolepsis and metamorphosis in particular allowed Linnaeus to account for much variation that was not relevant to his classification but

that nevertheless existed and so could not be entirely dismissed. This point is a very important one. As Guédès (1969) correctly observed, in this new way of looking at a plant, Linnaeus paid close attention to teratological phenomena and similar variation that he necessarily ignored when working on the limits of genera in the sexual system. Examples of the term "varietas" included double and proliferous flowers and other trivial variation of no taxonomic importance (Linnaeus, 1744). Luxuriant flowers, including both the double and proliferous flowers mentioned above, were always monstrous, never natural (Linnaeus, 1751a). All double flowers were at most varieties, and variety never could be the basis of real species (Linnaeus, 1762b). This was reasonable from Linnaeus's taxonomic viewpoint. The essences of species never changed, so how could these variants, the expression of which often depended on the fertility of the ground in which they were grown, represent that essence? (However, see Ramsbottom, 1939.) In Linnaeus's morphological work they could, however, be evidence of the potentiality of plant form. In this alternative way of understanding plants, what is accidental variation in one situation becomes important evidence of the real nature of structure in another.

As with Goethe, there is no clear idea of a type[14] or ideal plant in Linnaeus's morphological writings; there is simply a continuum of form. Although at first sight all appendicular organs are best interpreted as modified leaves (this is a reading of some passages in Linnaeus—e.g., 1760c, p. 19), this would seem to run counter to Linnaeus's statements that the anthers, stigmas, and seeds were the essential parts of the flower: how could structures essential at high levels of classification be modified from those essential only at low levels? However, since Linnaeus noted that the medulla was involved in the production of all appendicular organs, the leaf or calyx could be considered simply as two parts of the "shoot" from the cortex modified by the medulla; the taxonomically most important structures were those closest to the maternal forces in the medulla.

Thus the form-making potentiality of the plant largely or entirely resided in the cortex, although for its expression in visible form involvement of the cortex with the medulla was essential. That the pistil (largely pure medulla) changed its form in some terata is not to be interpreted as a demonstration of the interchangeability of medulla and cortex (cf. Guédès, 1969) but simply as the medulla failing to penetrate the cortex or penetrating it more strongly than was usual in a flower (a discussion on staminate flowers is along the same lines—Linnaeus, 1763). The medulla stimulated the production of organs appropriate to the balance of physiological forces in the plant, only in the pistil perhaps in part determining form. Otherwise the medulla itself was largely formless; even in the flower it could be argued that carpels took different forms, especially in terata, because they had a thin cortical covering, although Linnaeus does not seem to have gone that far.[15] However, his explanation of the malleability of

[14]As Brady (1987) and some others (e.g., Lenoir, 1987) have rightly emphasized, there is also no notion in Goethe's early botanical work of a definite form that is the "type" of all appendicular structures and to which all others must ultimately be reducible; all appendicular organs are not modified leaves, or modified anything else for that matter (see also Arber, 1946).

[15]Guédès (1969) thought that Linnaeus's flower was polyaxial, but this seems too "modern" an interpretation. As we saw, Linnaeus did not distinguish clearly between axillary and terminal buds.

form in species of *Chaos* and his theory of hybridization, in which God created a single medulla that became differentiated only by contact with a series of different cortices during successive hybridizations, confirm that pure medulla lacked particular form.

Hence Linnaeus had achieved a fairly comprehensive explanation of the material cause of form. The substance of the organism (cortex) was dissociated from the essence (medulla) that generated the form that substance assumed, and essence became manifest in substance. The efficient cause of plant form is the physiological-balance theory described above. But hybridization and continuity compromise any attempt to make simplistic explanations of the later Linnaeus as being a rigid typologist.

One strand of thought in pure morphology is an emphasis on the continuity of form, as illustrated by the comparison of different organs showing intermediate structures more or less out of any context supplied by the taxonomic relationships of the organisms bearing those organs (see Stevens, 1984c). It is this kind of continuity that is evident in Linnaeus's morphological writings. The "plenitudo" that he emphasized (Linnaeus, 1755a, p. 7) is both a simple fullness or doubling of a flower and also a phenomenon that leads to the confirmation that there is continuity or plenitude in the world of pure form. Morphological plenitude in particular interrelated a number of diverse phenomena in the world of plant form; unruly form was at least reduced to order, even if not completely understood. Indeed, the "Linnaean" cortex-medulla theory of plant tissues and the physiological-balance theory of the vegetative-floral distinction provided him with a rather full and complex understanding of form. His work on what we would call pure morphology concentrated more on nature's similarities than on its differences and led him to an apparently satisfying and truly systematic comprehension of the plant world.

But Linnaeus was also the quintessential classifier and namer, and here he proceeded in a largely analytical fashion. Yet despite these extensive and time-consuming classificatory studies on which he dealt with the flood of novelties pouring into Uppsala from correspondents around the globe, he attempted the partial synthesis of a world of systematically grouped form as a continuum, at least at the suprageneric level (e.g., Linnaeus, 1737, 1751a; Linnaeus's correspondence with Albrecht von Haller--see Smith, 1821, Vol. 2; Daudin, 1926).[16] As already noted, hybridization—in which the cortex-medulla theory played an important, if poorly understood, role—could generate this continuity. It explained the arrays of similar species being discovered in genera like *Geranium* and *Erica* and the lack of distinction between genera assembled into natural groups (Linnaeus, 1744 (see Ramsbottom, 1939), 1762b). At a yet higher taxonomic level, the cortex-medulla theory and prolepsis together enabled Linnaeus to demonstrate that a number of animals were like plants in important respects, and so continuity was evident there as well (see TABLE 2). New discoveries in

[16]Since many plants remained to be discovered, Linnaeus had a ready explanation for apparent gaps. Such gaps are clear in the diagram of relationships of Linnaeus's *ordines naturales* (families), believed to be based on one drawn by Linnaeus himself (Giseke, 1792). Some families touch, but most are separated by gaps of varying sizes.

the microscopic world hardly disturbed the link between *Hydra,* with its sensitive flowers, and the other Zoophyta, with flowering plants. *Volvox chaos* was well positioned. The dissolution of form it seemed to suggest in its terminal position in the animal kingdom was not the change from animals to plants, which was a gradual change rather than dissolution anyway, but the loss of form that heralded the discovery of a new kingdom. In its formlessness, capacity for increase, and activity was evidence of the very principles of life, life in its purest and certainly simplest form—pure medulla (see also Broberg, 1985).

The cortex-medulla theory or, more generally, Linnaeus's ideas on the construction of organisms also helped his understanding of how and why organisms could live together in the world (i.e., order between organisms in the living world; it was used to explain a yet higher level of causality) (see, for example, Lindroth, 1983). Many of the properties of plants, including their palatability to insects and, perhaps not surprisingly, their medicinal attributes (Linnaeus, e.g., 1747, 1752; Giseke, 1792),[17] are constant in genera and higher groups in a natural classification. Such properties reside in the medulla, which is at the same time at the heart of natural classifications in general. The close association between plants and insects was evident in that some insects tended to eat plants of different species of the same genus (Linnaeus, 1752; 1760a); perhaps insect larvae could teach us about the medicinal properties of plants (Linnaeus, 1749; see also Linnaeus, 1751b). This close, although rather one-sided, association was strengthened for Linnaeus because the larvae of both groups metamorphosed to produce the adult, hence the listing of both insects and plants in the thesis *Pandora et Flora Rybyensis* (Linnaeus, 1771). Such an interlocking of ideas would allow Linnaeus at least partially to sidestep the issue of whether God had created a definite number of species; even if he had not, hybridization might not increase the number of different ecological or functional units in nature. Commenting on the later Linnaeus, Broberg (1985, p. 180) remarked: "What he needed was a principle which gave causality to creation, not blind faith." That principle was largely based on the cortex-medulla theory.

Linnaeus's world of systematic continuity was different in nature from that of morphological continuity. Although both are to an extent based on the cortex-medulla theory, the latter more directly than the former, they use different observations to support the different constructions of continuity. Linnaeus would surely have approved of the comment that P. J. F. Turpin (1815, p. 429) made when discussing possible interrelationship of inflorescence types: "But why have we need to make abstractions, since nature never fails to show herself all the intergradations which can illuminate us?" (Early in his life in particular, Turpin was strongly influenced by Goethe.) There is little evidence of discord between the two kinds of continuity in Linnaeus's own work; both stemmed from his observations of nature. As a further complication, genera

[17]The opposition between the masculine, external, vital cortex and the feminine, internal, animal medulla is the key to Linnaeus's concept of medicine. Since it also involves an opposition between taste and smell and a hefty dose of numeralogy (the number 5 again), Linnaean medicine is less than easy to understand (Linnaeus, 1766b; see also Hjelt, 1907; Lindroth, 1983).

and higher taxa that in the taxonomic scheme of things needed to be separated by distinctive and constant features were associated in an arrangement of a kind that allowed the reader to develop ideas of continuity and even change—as also in Charles Bonnet and J. B. A. P. M. de Lamarck (see Lovejoy, 1936—he barely mentioned Linnaeus). Further, prolepsis, metamorphosis, and hybridization are more directly subversive of a world of discrete, separate entities. The tension is however, evident to us, the tension between nature dynamic and flexible and nature ordered rationally, preferably with gaps.

Historically, however, there has all too often been overt or covert conflict between systematists and evolutionists (the work of the latter is dependent for a considerable part on the systematic patterns produced by the former) and proponents of pure morphology (see, for example, Cusset, 1982; Wetzels, 1985; Appel, 1987; Brady, 1987; Portmann, 1987). Wetzels (1985, p. 145) wrote eloquently about Goethe's approach: "It is this delicate simultaneity of the concrete immediacy of individual observation and the equally concrete presence of a picture of a whole, that Goethe had described earlier as 'tender empiricism,' an empiricism which was capable of making the individual phenomenon transparent so that the whole of which it was not so much a part, but a manifestation, became visible." But of course words such as "empiricism" and the like have different meanings for proponents of these two approaches; there are tensions between the phenomenological Goethean and the somewhat-more-circumscribed Linnaean approaches to morphology (see above) and more conventional systematics and science (see Amrine & Zucker, 1987; Sattler, 1986). The form of the organism may not have the same meaning or significance for the proponents of the two approaches. Lindroth's (1983) important essay almost casually captures this dilemma. He emphasized that Linnaeus was preeminently an empiricist, an acute and enthusiastic observer, a voluptuary of nature, and an empirical genius, yet somebody who made no major contributions to science. In his systematic work empiricism was subservient to an overwhelming desire for order. Yet in the cortex-medulla theory an almost "tender empiricism" combines with order because the theory explains why and how the world is as it is. As a theory, it proved to be of little interest even to his contemporaries. Linnaeus's way of establishing order, as Lindroth so clearly demonstrated, was hasty, superficial, and to a high degree inductive, as well as being based on a questionable philosophy of life.

The conflict is less evident in Goethe's work. As is well known, he had earlier found the Linnaean system, and the terms associated with it, intellectually unsatisfying. Goethe disliked counting and analyzing, which he thought that Nature abhorred, but these were needed if he was to use the Linnaean system. Goethe also observed how the same organ varied in shape on a single plant, and to him this suggested problems with terminological categorization (see, e.g., Arber, 1946; Guédès, 1969; Wetzels, 1985). Of course, the Linnaean sexual system was not the most natural arrangement when it came to the delimitation of larger groupings of plants (cf. Stafleu, 1971), although a few groups, such as the Gynandria-Diandra, the Didelphia-Decandra, and the Tetradynamia-Siliculosa were more or less composed of related genera (Orchidaceae, Leguminosae, and Cruciferae, respectively; see Linnaeus, 1753). Thus, neither the terms

Linnaeus used for plant parts nor Linnaeus's sexual system itself led Goethe to a satisfactory understanding of plant form or diversity. However, his ideas on metamorphosis did just this, albeit in a largely asystematic context.

Goethe and Linnaeus drew the data they synthesized into their respective visions of continuity—metamorphosis, prolepsis, a modified *scala naturae*—from their appreciation of the world of external form. Belief in the continuity of organic form persisted in the systematic community well into the nineteenth century; it was believed, echoing Linnaeus, that if there were gaps in the system of nature, they would eventually be filled. But the similarities go further. Linnaeus's valuation of anatomy resonates with the work of A.-L. de Jussieu, a founder of the new "natural method" in systematics. For De Jussieu (1778) the functions of the relatively few plant structures that were used in classification were known; those structures were almost all external, and there was no need to study their anatomy. Of course, his remarks were made in a systematic context, and those of Linnaeus some 20 years before in a largely morphological context, yet both men emphasized the external appearance of the plant as being a suitable object for study, and the two produced natural arrangements that are similar in their basic principles. The world of external form may turn out to be an unreliable guide to both systematics and anatomy, and continuity in one guise or another, or at least reticulating relationships, are the likely results of an analysis of external form. De Jussieu's natural method is as explicitly based on assumptions of continuity as Linnaeus's conception of life, and his *Genera Plantarum* (De Jussieu, 1789) can be analyzed in the same way as Linnaeus's Vermes, and with similar results.

Linnaeus, with a view of life notably archaic or anachronistic even for its time (see, for example, Cain, 1958; Stafleu, 1971; Lindroth, 1983; Hull, 1985), embraced the Aristotelian notion of plenitude and worked it out in the context of a natural arrangement of groups, the characters of which were all to be discerned by the naked eye. The hylomorphic cortex-medulla theory aids in our understanding of this natural arrangement. It provides features that serve to bind the larger units of the arrangement into an indivisible, albeit branching, continuum rather than to separate them, in the process showing clearly that the units are not discrete. It also justified the selection of characters used in classification. In a similar fashion, Linnaeus developed an approach to the analysis of plant form that embraced another manifestation of plenitude, the fundamental similarity and interconvertibility of the appendicular organs of the plant. The rather archaic basis of this thought should not blind us to its evident power in synthesizing a very disparate body of observations.

It is noteworthy that the cortex-medulla theory is best developed in plants and fungi. For plants, Linnaeus based his ideas on his own observations of exterior form and on Cesalpino's seventeenth-century theory, largely ignoring the work of Grew and Malpighi; for fungi, his thoughts were sparked by Münchhausen's disputed findings. In animals, the theory is most evident in Linnaeus's discussion of the least-understood and smallest organisms, albeit those on which some of the most exciting discoveries of the day were being made. It was most successful where knowledge was least well established, serving to guide him through these areas of uncertainty; the theory colored both his

observation and his interpretation of other people's data (see Le Guyader, 1988). As with the "*nemesis divina,*" "reality must—once again—adjust itself to the scheme" (Lindroth, 1983, p. 53).

Linnaeus's theory was epitomized in the name changes of that almost animal, almost plant, almost a member of a new kingdom: *Volvox chaos* became *Chaos proteus*. *Chaos* itself was a genus of half-misinterpreted observation at the limits of one particular man's late-eighteenth-century vision. The fate of Linnaeus's theory was like that of *Furia,* a new genus described by Linnaeus and placed adjacent to *Chaos* in the twelfth edition of the *Systema Naturae* (see Lindroth, 1983). The sole species in the genus, *Furia infernalis,* was Linnaeus's contribution to the book of imaginary beings; it never existed, despite the fact that a vicar, no less, reported that one had fallen onto his plate. The vicar and Linnaeus alike were mistaken, and as we saw above, De Candolle rejected the cortex-medulla theory because monocotyledonous plants simply did not have pith. Similarly, J. G. Kölreuter's experiments on hybridization (see Roberts, 1929; Mayr, 1986) showed that crosses in which the same species was first the female parent, and then the male parent, tended to produce the same kind of hybrid: there was no maternal dominance; there was not even any hybridization. Even so, ideas of metamorphosis in particular and change in general are so pervasive in Linnaeus's later works that their influence should not be entirely discounted.

ACKNOWLEDGMENTS

We are very grateful to K. Boss, G. Broberg, A. J. Cain, A. H. Dupree, D. Hendler, A. Kabat, J. L. Larson, E. Lord, R. J. O'Hara, D. H. Pfister, S. A. Roe, and R. Turner for comments on the manuscript and/or helpful discussion during its preparation. Our thanks are also due to Ihsan Al-Shehbaz for preparing the diagram, to John Lupo for taking the photographs, to the staff of the libraries in the Harvard University Herbaria for their unfailing help, and most especially to Rose Balan and Oanh Tran for typing the manuscript. Finally, we also owe a great deal to the tolerant and helpful audiences that have listened to versions of these complex ideas.

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A REVISION OF WEBERBAUERA (BRASSICACEAE)

IHSAN A. AL-SHEHBAZ[1]

Sixteen species of *Weberbauera* are recognized, and the genera *Alpaminia, Pelagatia,* and *Stenodraba* are placed in the synonymy of *Weberbauera. Weberbauera cymosa, W. densifolia, W. minutipila, W. retropila,* and *W. smithii* are described as new. The new combinations *W. chillanensis, W. colchaguensis, W. herzogii, W. imbricatifolia, W. lagunae, W. parvifolia, W. stenophylla,* and *W. suffruticosa* are proposed.

Schulz (1924, 1936) placed *Weberbauera* Gilg & Muschler (two species) and its closest South American relatives, *Alpaminia* O. E. Schulz (monotypic), *Pelagatia* O. E. Schulz (monotypic), and *Stenodraba* O. E. Schulz (six species), in subtribe Pachycladinae O. E. Schulz of the tribe Sisymbrieae DC. The subtribe, which consists of a heterogeneous assemblage of 15 genera, is artificially delimited and is based primarily on its having siliculose instead of siliquose fruits. All four genera above have siliquose fruits that are basically similar to those assigned by Schulz to other subtribes of the Sisymbrieae. A critical study of the whole tribe is needed before meaningful realignments of its genera on a broad scale can be proposed. However, progress is made in this direction in the following treatment of some of its South American members.

Schulz (1924, 1936) distinguished *Stenodraba* from *Alpaminia, Pelagatia,* and *Weberbauera* solely by its ebracteate instead of bracteate inflorescences and then separated *Weberbauera* from both *Alpaminia* and *Pelagatia* by its allegedly slender instead of flattened funicles. As argued by Macbride (1934), however, funicle thickness is insufficient grounds for delimitation of genera. In fact, it is an erroneous distinction. Almost all plants of *W. spathulaefolia* (A. Gray) O. E. Schulz (the type of *Weberbauera*) that I have examined, including those annotated by Schulz, have flattened funicles indistinguishable from those of *Alpaminia* and *Pelagatia.* The last two genera are also very similar to *Weberbauera* in habit, as well as in various aspects of the flower and fruit. A casual observer might argue that the occurrence in *Alpaminia* of malpighiaceous trichomes (see FIGURE 1a) and cymelike racemes is sufficient for the recognition of a distinct genus. But submalpighiaceous, subsessile or short-stalked trichomes are found in *W. spathulaefolia* (see FIGURE 1b) and in *W. parvifolia* (Phil.) Al-Shehbaz, and cymelike racemes are also characteristic of *W. cymosa* Al-Shehbaz, a species not closely related to *Alpaminia.* Therefore, neither the nature of the trichomes nor the inflorescence type supports the separation of *Alpaminia* from *Weberbauera.*

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Journal of the Arnold Arboretum **71:** 221–250. April, 1990.

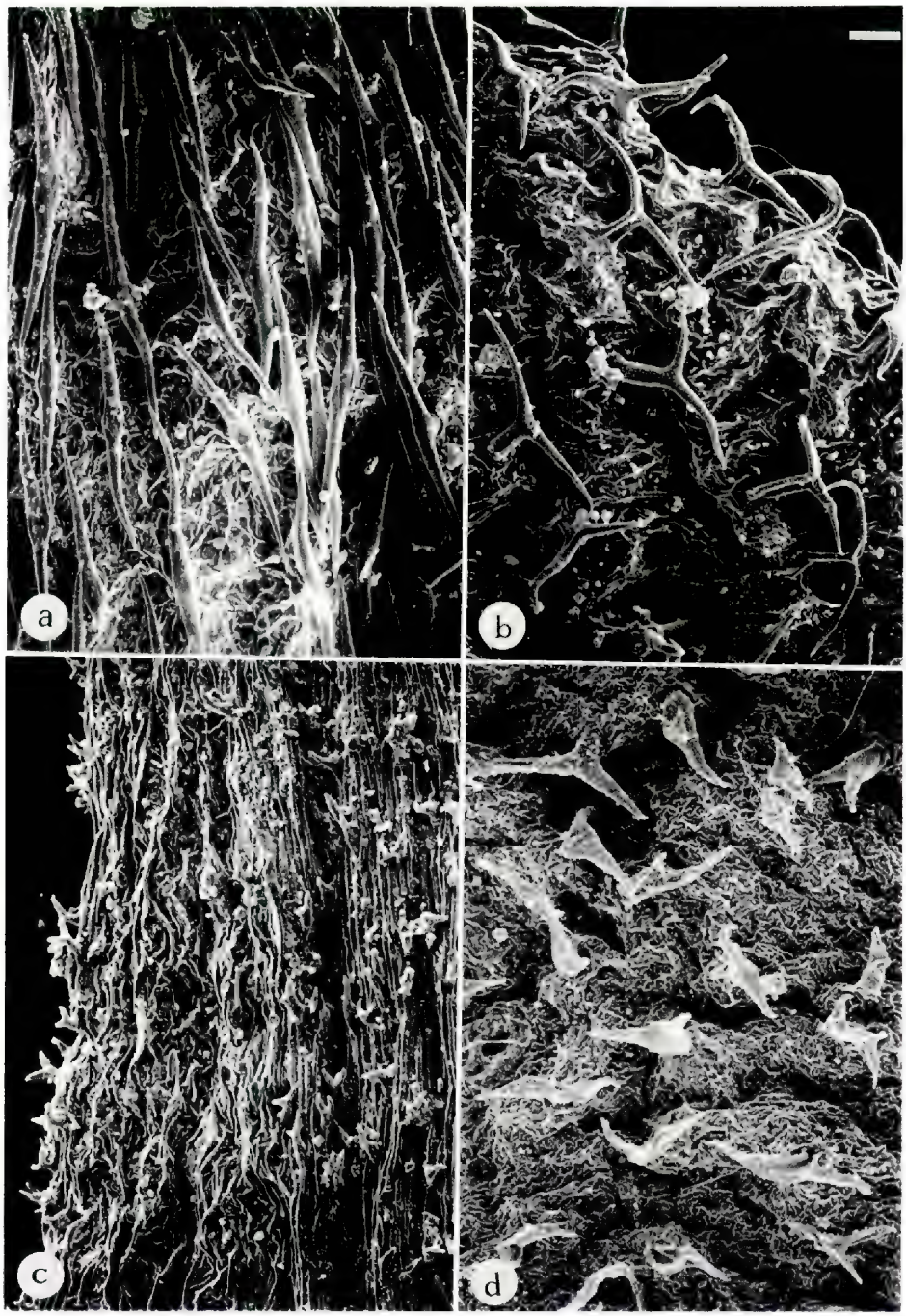


FIGURE 1. Leaf surfaces of *Weberbauera*: a, *W. trichocarpa* (*Macbride 3073*, GH); b, *W. spathulaefolia* (*Smith, Valencia, & Torres 11845*, GH); c, *W. minutipila* (holotype); d, *W. retropila* (holotype). Scale bar = 100 μm.

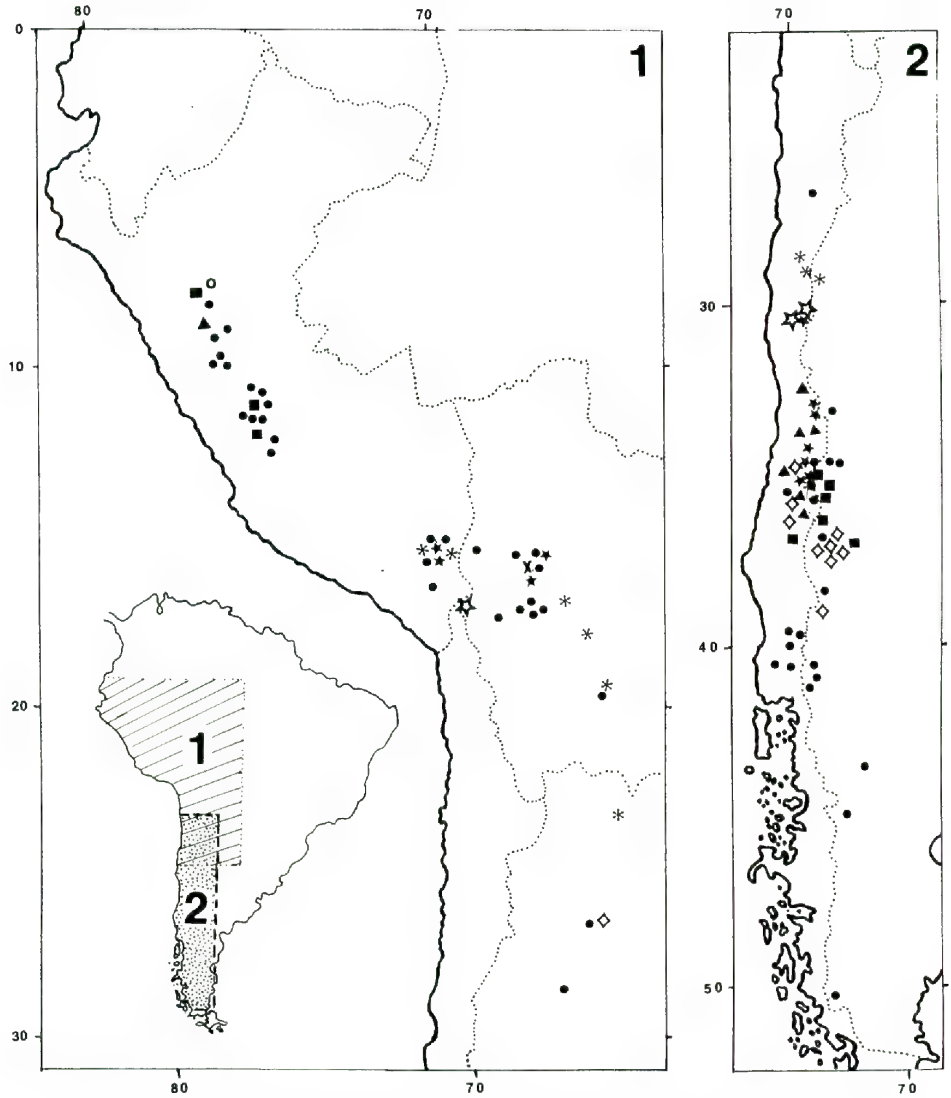
Pelagatia was not founded on well-observed characters, and its reduction by Macbride (1934, 1938) to synonymy of *Weberbauera* is fully justified. *Pelagatia bracteata* O. E. Schulz, hereafter *W. bracteata* (O. E. Schulz) J. F. Macbr., belongs to a group of species that forms the core of *Weberbauera,* and it appears to be a sister species of *W. herzogii* (O. E. Schulz) Al-Shehbaz.

Schulz's (1924, 1936) separation of *Stenodraba* from *Weberbauera* on the basis of its having ebracteate instead of bracteate inflorescences is misleading and unreliable. The holotype of *W. spathulaefolia* consists of two plants, of which one has an ebracteate inflorescence and the other has only the lower half of the raceme bracteate. As is shown below, in *W. spathulaefolia* the portion of the inflorescence that is bracteate is highly variable, and a continuous variation from fully bracteate to completely ebracteate individuals can be found within the same population. Furthermore, numerous genera of the Brassicaceae (e.g., *Arabis* L., *Cardamine* L., *Draba* L., *Sisymbrium* L., *Streptanthus* Nutt.) include some species with ebracteate and others with bracteate inflorescences. In general, it is unsound to delimit genera in this family solely on the basis of presence vs. absence of bracts. *Stenodraba* is also indistinguishable palynologically from *Weberbauera* (Al-Shehbaz, unpublished). Because there is not a single reliable character that separates *Stenodraba* from the earlier-published *Weberbauera,* the two genera are here united.

Ravenna's (1981) transfer to *Stenodraba* of four species previously included in *Sisymbrium* requires careful evaluation. These species were placed in his newly created sect. *Elatia* Ravenna, which was distinguished from sect. *Stenodraba* in having erect stems and much-branched inflorescences instead of somewhat decumbent stems and unbranched inflorescences. In addition, sect. *Elatia* often has long, slender fruiting pedicels and subglobular floral buds. As I interpret it, no species of *Weberbauera* (including *Stenodraba*) has any of these features. I disagree with Ravenna (1981) in assigning members of sect. *Elatia* to *Stenodraba,* because they are unrelated to any of the 16 species that fall naturally into *Weberbauera.* A critical evaluation of the species assigned to this section reveals that all except one are better retained in *Sisymbrium.*

Although the limits of *Weberbauera* are expanded here beyond those previously recognized, the genus is well defined and apparently monophyletic. However, as is the case in many other genera of the Brassicaceae, it is not possible in *Weberbauera* to identify the shared derived characters (synapomorphies) that readily unite its members. Species of *Weberbauera* are low, cespitose perennials with simple or branched caudices, well-developed rosettes, usually persistent petiolar bases, usually unbranched, subdecumbent stems, nonsaccate sepals, ringlike nectar glands that subtend the bases of all stamens, oblong to linear fruits, wingless seeds, incumbent cotyledons, and usually thickened funicle bases. None of these features is unique to *Weberbauera,* but no other South American genus has this combination of characters.

Weberbauera grows primarily along the Andes and is distributed from northern Peru south through western Bolivia, central Chile, and western Argentina into Patagonia (see Maps 1, 2). The highest concentration of species is in Peru



MAPS 1, 2. Distribution of *Weberbauera*: 1, *W. bracteata* (circle), *W. cymosa* (X), *W. densifolia* (diamond), *W. herzogii* (asterisks), *W. minutipila* (solid stars), *W. retropila* (hollow star), *W. smithii* (triangle), *W. spathulaefolia* (dots), and *W. trichocarpa* (squares); 2, *W. chillanensis* (squares), *W. colchaguensis* (dots), *W. imbricatifolia* (triangles), *W. lagunae* (asterisks), *W. parvifolia* (diamonds), *W. stenophylla* (solid stars), and *W. suffruticosa* (hollow stars).

and Chile, where eight and seven species grow, respectively. Except for *W. colchaguensis, W. herzogii,* and *W. spathulaefolia,* the other species of *Weberbauera* either are highly localized endemics or are narrowly distributed.

Chromosome numbers are known only for *Weberbauera spathulaefolia,* a

species reported to have $2n = 52$ (Diers, 1961). Attempts to obtain mitotic counts from the root tips of a few species that I grew at Cambridge were unsuccessful.

Weberbauera was originally described by Gilg & Muschler (1909) as a monotypic genus. Schulz (1924) was correct in reducing the name of its original type, *W. densiflora* (Muschler) Gilg & Muschler, to synonymy of the earlier-published *Sisymbrium spathulaefolium* A. Gray, which he transferred to *Weberbauera*. Therefore, *W. spathulaefolia* (A. Gray) O. E. Schulz becomes the generic type.

The present study has included a critical examination of authentic material of almost all taxa. This has helped immensely in the interpretation of species and generic limits, as well as in the proper placement of synonyms. I have been very fortunate in this regard because such an opportunity was not available to others who have studied this group of plants.

TAXONOMY

Weberbauera Gilg & Muschler, Bot. Jahrb. Syst. **42**: 481. 1909. TYPE: *W. densiflora* (Muschler) Gilg & Muschler = *W. spathulaefolia* (A. Gray) O. E. Schulz.

Alpaminia O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 191. 1924. TYPE: *A. trichocarpa* (Muschler) O. E. Schulz.

Pelagatia O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 192. 1924. TYPE: *P. bracteata* O. E. Schulz.

Stenodraba O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 186. 1924. LECTOTYPE (designated by Ravenna, 1981): *S. chillanensis* (Philippi) O. E. Schulz.

Cespitose, perennial herbs; caudices simple or branched, usually covered with petiolar remains of previous years. Trichomes simple or furcate, rarely malpighiaceous. Stems few to several, usually subdecumbent, or decumbent, rarely ascending, unbranched, glabrous or pubescent. Basal leaves petiolate, usually forming well-defined rosettes that terminate caudex branches; blades entire or dentate, rarely pinnately lobed, often ciliate; petioles usually persistent; cauline leaves few or several, rarely lacking. Inflorescences few- to many-flowered, bracteate or ebracteate, corymbose racemes, rarely modified and cymelike, usually elongated in fruit. Sepals cauducous or rarely persistent, usually erect, oblong to ovate, nonsaccate, scarious at margin, glabrous or pubescent. Petals white, spatulate to oblong, usually attenuate into clawlike base. Nectar glands confluent, low, ringlike, subtending bases of all stamens. Stamens 6, slightly tetradynamous. Fruits dehiscent, oblong to linear, terete or somewhat flattened, smooth or rarely slightly torulose, usually with prominent midvein; septa hyaline, complete; styles conspicuous to obsolete; stigmas entire. Seeds uniseriately or rarely subbiseriately arranged in each locule, oblong, wingless; cotyledons incumbent; funicles thick or flattened at placental end, slender distally.

KEY TO THE SPECIES OF WEBERBAUERA

A. Plants, including fruits, densely covered with sessile, medifixed, malpighiaceous trichomes; petal claws often pubescent. ..... 9. *W. trichocarpa.*

A. Plants glabrous or pubescent with simple and/or stalked furcate trichomes; fruits glabrous or rarely sparsely pubescent with simple trichomes; petal claws glabrous.

B. Inflorescences bracteate throughout.

C. Basal leaves conspicuously ciliate with simple trichomes.

D. Fruits attenuate, styles (0.8–)1.2–2.5 mm long; petals 3.5–5(–7) mm long; basal leaves entire or rarely dentate. ..... 6. *W. herzogii.*

D. Fruits obtuse, styles to 0.2 mm long; petals 2.5–3 mm long; basal leaves lyrate-pinnatifid. ..... 7. *W. bracteata.*

C. Basal leaves not ciliate, sometimes glabrous or with some furcate trichomes. ..... 1. *W. spathulaefolia.*

B. Inflorescences ebracteate, with lowermost flowers rarely bracteate.

E. Sepals persistent; fruits sparsely pubescent with retrorse, simple trichomes. ..... 5. *W. retropila.*

E. Sepals soon caducous; fruits glabrous.

F. Basal leaves numerous; petioles persistent, straw colored, 3–3.5 cm long, about as long as blades, overlapping and forming dense crown. ..... 2. *W. densifolia.*

F. Basal leaves few to many; petioles soon caducous or if persistent, then not straw colored, usually less than 3 cm long, shorter than blades, not forming dense crown.

G. Stems usually branched above; plants with some dendritic trichomes. ..... 16. *W. parvifolia.*

G. Stems usually unbranched above; plants without dendritic trichomes.

H. Basal and cauline leaves ciliate with simple trichomes.

I. Basal leaves pinnatifid, with 3 to 5 pairs of lateral lobes; inflorescences modified, 1- to 3-flowered, cymelike racemes; petals less than 2 mm long; caudices unbranched; stems less than 2 cm long. ..... 8. *W. cymosa.*

I. Basal leaves entire, rarely dentate or sinuately lobed; inflorescences usually many-flowered racemes; petals 2–5.5 mm long; caudices much branched; stems more than 2 cm long.

J. Basal leaves semiterete, thick, linear. ..... 14. *W. suffruticosa.*

J. Basal leaves flat, thin, oblong to oblanceolate or spatulate, rarely linear-lanceolate.

K. Styles obsolete or rarely up to 0.6 mm long in fruit.

L. Fruits torulose; infructescences lax racemes; fruiting pedicels slender, divaricate, 4–8(–12) mm long; basal leaves entire, to 1.5 mm wide. ..... 13. *W. lagunae.*

L. Fruits smooth; infructescences usually dense, subumbellate; fruiting pedicels stout, subappressed, 1.5–4.5(–7) mm long; basal leaves usually dentate, 2–4.5(–6) mm wide. ..... 10. *W. colchaguensis.*

K. Styles 1–3 mm long in fruits, if shorter then fruits conspicuously flattened.

M. Lower surfaces of basal leaves usually with trichomes shorter than those on margins or upper surfaces; fruits torulose; stems usually leafless; petioles of basal leaves stout, swollen. ..... 15. *W. imbricatifolia.*

M. Lower surfaces of basal leaves glabrous; fruits smooth; stems with few leaves; petioles of basal leaves slender, not swollen.
N. Basal leaves entire; petals (3.5–)4–5 mm long; styles (0.8–)1.5–2 mm long in fruit. ..... 12. *W. stenophylla.*
N. Basal leaves dentate; petals 2.5–3.5 mm long; styles 0.5–0.9(–1.1) mm long in fruit. ..... 11. *W. chillanensis.*

H. Basal and cauline leaves not ciliate, sometimes glabrous or pubescent with at least some branched trichomes.
O. Leaves fleshy, glabrous; petals 6.5–8 mm long; caudices thick, 1.5–2 cm in diameter. ..... 4. *W. smithii.*
O. Leaves not fleshy, often pubescent or rarely glabrous; petals 2–3.5(–4) mm long; caudices slender, almost always less than 1 cm in diameter.
P. Trichomes minute, 0.03–0.1(–0.15) mm long; basal leaves filiform to narrowly linear; cauline leaves coarsely dentate-serrate. ..... 3. *W. minutipila.*
P. Trichomes coarser, (0.2–)0.4–0.7(–1.1) mm long; basal leaves oblong, ovate, lanceolate, or spatulate, very rarely linear; cauline leaves entire to repand or dentate. ..... 1. *W. spathulaefolia.*

1. **Weberbauera spathulaefolia** (A. Gray) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 193. 1924.

Sisymbrium spathulaefolium A. Gray, U.S. Expl. Exped. Phan. **15**(1): 60. 1854. *Hesperis spathulaefolia* (A. Gray) Kuntze, Revis. Gen. Pl. **2**: 935. 1891. TYPE: Peru, [Junín,] Obrajillo, Wilkes Expedition, without collector's name (holotype, US *5526*!; isotype, NY!).

Arabis spathulata Walp. *in* Meyen, Observ. Bot. 248. 1843, non *A. spathulata* DC. Syst. Nat. **2**: 227. 1821, non Nutt. ex Torrey & A. Gray, Fl. N. Am. **1**: 81. 1838. TYPE: Peru, Altos de Toledo, *Meyen s.n.*, April 1831 (not seen).

Sisymbrium orophilum Wedd. Ann. Sci. Nat. Bot. V. **1**: 288. 1864. *Hesperis orophila* (Wedd.) Kuntze, Revis. Gen. Pl. **2**: 935. 1891. TYPE: Bolivia, Prov. Larecaja, vicinity of Sorata, near Anilaya, Juriguana, 4500 m alt., *Mandon 914 bis* (holotype, P!; isotypes, BM!, G!).

Sisymbrium oliganthum Wedd. Ann. Sci. Nat. Bot. V. **1**: 289. 1864. TYPE: Bolivia, rochers de La Laucha, Cordillera de La Paz, *Weddell s.n.*, 1851 (holotype, P!).

Sisymbrium septaceum Wedd. Ann. Sci. Nat. Bot. V. **1**: 289. 1864. TYPE: Bolivia, Potosí, *D'Orbigny 1447* (holotype, P! (photo, F!)).

Braya densiflora Muschler, Bot. Jahrb. Syst. **40**: 275. 1908. *Weberbauera densiflora* (Muschler) Gilg & Muschler, Bot. Jahrb. Syst. **42**: 481. 1909. TYPE: Peru, Hacienda Arapa, Yauli, Lima–Oroya road, 4400 m alt., *Weberbauer 304* (lectotype (designated by Macbride, 1938), B!; isolectotype, G!).

Weberbauera spathulaefolia (A. Gray) O. E. Schulz var. *integrifolia* O. E. Schulz, Publ. Field Mus. Nat. Hist. Bot. Ser. **8**: 80. 1930. TYPE: Peru, [Depto. Lima,] Río Blanco, in rocks, uplands, 8–19 May 1922, 15,000 ft [4572 m] alt., *Macbride & Featherstone 811* (holotype, F! (photos, F!, G!, GH!); isotype, GH!).

Caudices simple or sometimes branched, slender, less than 1 cm in diameter, usually covered with petiolar remains of previous years. Stems usually decumbent, unbranched, (2–)4–23(–43) cm long. Trichomes (0.2–)0.4–0.7(–1.1) mm

long, short stalked and submalpighiaceous, or long stalked and furcate, sometimes simple, rarely absent. Basal leaves petiolate; blades oblong or lanceolate to spatulate, rarely linear to ovate, (1–)2–6(–7) cm long, (2–)3–9(–11) mm wide, obtuse or rarely acute at apex, entire or repand to dentate, rarely lyrately pinnatifid, thin and nonfleshy, pubescent or glabrous; petioles (0.5–)1–4.5 cm long. Cauline leaves subsessile to short petiolate; blades oblong to obovate or lanceolate, 5–13(–18) mm long, 2–8(–15) mm wide, entire to repand or dentate. Inflorescences bracteate to ebracteate; infructescences lax to compact, (0.5–)1–9(–17) cm long. Sepals caducous, oblong to ovate, (1.5)2–2.5(–3) mm long, 1–1.4(–1.7) mm wide, obtuse, scarious at margin, sparsely pubescent to glabrous. Petals white, spatulate, attenuate to clawlike base, 2–3.5(–4) mm long, 1.5–1.8(–2) mm wide. Filaments white, erect, 1.5–2.5 mm long, somewhat dilated at base; anthers oblong to ovate, 0.4–0.7 mm long. Fruiting pedicels ascending, subappressed at base, straight to curved, (2–)3–6(–8) mm long. Fruits divaricate to erect and subappressed to rachis, linear to oblong, terete, nontorulose, usually abruptly ending in style, straight or rarely curved, (6–)8–15(–20) mm long, 1.5–1.8(–2) mm wide; valves smooth, glabrous, conspicuously to obscurely veined; septa hyaline; styles 0.2–0.8(–1.5) mm long; stigmas entire. Seeds subbiseriately arranged, oblong to ovate, (0.8–)1–1.4 mm long, (0.5–)0.6–0.8 mm wide, light to dark brown; funicles usually strongly differentiated into persistent broad base and filiform distal portion.

Flowering late December to mid-February, fruiting late February to mid-May. Growing on sand or clay in puna-grassland, boggy areas, valley bottoms, calcareous cliffs, dry steep slopes, and rocky places at altitudes of 3600–4800 m.

REPRESENTATIVE SPECIMENS EXAMINED. **Argentina.** PROV. CATAMARCA: Depto. Andalgala, Cerro Yutuyaco, *Sleumer 2721* (LIL); Río Potrero, *Sleumer 1905* (B). PROV. JUJUY: Depto. Humahuaca, Mina Aguilar, *Sleumer 3402* (LIL). PROV. LA RIOJA: Sierra Famatina, Cueva de Pérez, *Hieronymus & Niederlein 376* (B). **Bolivia.** DEPTO. LA PAZ: Prov. Aroma, Huaraco Pendiente, *Fisel U-188* (GH), *U-472* (LPB); Prov. Larecaja, vicinity of Combaya, *Mandon 914* (BM, G, P); Prov. Murillo, La Cumbre, on road to Unduavi, *Solomon 5029* (MO); ca. 15 km NNE of La Paz, *Beck 9130* (GH); 17 km SE of Collana on La Paz–Calacoto road, *Beck 4290* (GH); Prov. Pacajes, Charaña, *Asplund 2664* (S, UPS), *6201* (US); Corocoro, *Asplund 2418* (S, UPS); Panacachi, *Asplund 2582* (S). DEPTO. POTOSÍ: Prov. Frías, Cerro Potosí, *Petersen & Hjerting 1030* (C, LIL), *Cárdenas 398* (US). **Peru.** DEPTO. ANCASH: Prov. Bolognesi, between Tallenga and Pachapaque, *Cerrate 749* (GH); Prov. Carhuás, Huascarán National Park [HNP], Quebrada Ishinca, *Smith, Valencia, & Gonzales 9440* (MO); Prov. Huarás, HNP, Quebrada Shallap, *Smith, Valencia, & Gonzales 9670* (MO); Prov. Huaylas, HNP, Quebrada Los Cedros, *Smith, Valencia, & Minaya 9924* (GH, MO); Prov. Recuay, HNP, pass between Nevado Pasto Ruri and Nevado Raría, *Smith & Escalona 10182* (MO); Quebrada Quena Ragra, *Smith, Valencia, & Torres 11730* (MO); Quebrada Queshque, *Smith, Valencia, & Torres 11845* (GH, MO); Río Pachacoto drainage, 15 mi from highway, *Smith, Stein, & Todzia 9373* (GH, MO). DEPTO. HUANCAVELICA: Prov. Huancavelica, Bunbunya, *Tovar 219* (GH). DEPTO. JUNÍN: between Cerro de Pasco and La Quinua, *Asplund 11871* (S); Morococha, *Haapala s.n.*, 15 Feb. 1949 (H); Ondores, *Pattersson 293* (S); vicinity of Oroya, *Kalenborn 132* (GH, NY), *132a* (US); between Tarma and La Oroya, *Weberbauer 2550* (B). DEPTO. LIMA: Río Blanco, *Macbride 2991* (F, NY); Saltacuna, *Soukup 1940* (US); Ticlio Bajo, *Diers 979* (GH); Visco, *Macbride & Featherstone 590* (F, G, NY); Prov. Huarochiri, Casapalca, *Asplund 11425* (S); Prov.

Yauyos, Huacrococha, 17 km to Tupe, *Cerrate 1226* (GH). DEPTO. MOQUEGUA: PROV. Moquegua, cordillera above Torata, *Weberbauer 7471* (BM, F, G, US). DEPTO. PASCO: PROV. Cerro, Cerro de Pasco, *Asplund 11779* (S), *Macbride 3065* (CAS, F, US). DEPTO. PUNO: PROV. Carabaya, Antapampa, *Vargas 6837* (F).

Weberbauera spathulaefolia is one of the most variable South American crucifers. The variation is most noticeable in length of infructescences, occurrence of bracts, type and density of trichomes, and shape and margin of leaves. The infructescences are usually racemes a few to several centimeters in length, but in *Asplund 11779* they are subumbellate and only 0.5 cm long, and in *Cerrate 749* they are lax and to 17 cm. Perhaps the most significant variation is in the length of the bracteate portion of the inflorescence. In many populations the inflorescences are either bracteate throughout or ebracteate, while in others only the lowermost portion of the racemes are bracteate. In some collections (e.g., *Asplund 2418, Macbride 2991*) both ebracteate and bracteate plants are found within the same population. As indicated above, the holotype of *W. spathulaefolia* has two plants; the raceme of one plant is ebracteate, while that of the other is bracteate only on the lower half. Evidently, the occurrence of bracts is not a good character for the generic delimitation of *Weberbauera.*

Stem and leaf pubescence of *Weberbauera spathulaefolia* is also highly variable. Glabrescent forms, as well as forms with simple or asymmetrically furcate trichomes, are widespread in specimens from throughout the range of the species. In contrast, plants with submalpighiaceous trichomes are apparently more common in the northern portions of the species range than elsewhere. However, in the majority of collections more than one trichome type is found, and in some (e.g., *Mandon 914*) both glabrous and densely pubescent plants are present.

Variation in the length of infructescences, the occurrence of bracts, and the pubescence of stems and leaves does not correlate with the geography of *Weberbauera spathulaefolia.* The species cannot be subdivided morphologically into practical subordinate taxa.

2. **Weberbauera densifolia** Al-Shehbaz, sp. nov. FIGURE 2.

Herba perennis caespitosa, radicibus longibus crassibus. Folia basales numerosa, petiolata, rosulata, petiolis persistentibus, rectibus, stramineis, 3–3.5 cm longis; lamina pinnatifida vel sinuata vel repando-dentata, 2–3 cm longa, 4–6 mm lata; folia caulina pauca, petiolata, repanda vel integra, 8–11 mm longa. Flores ingotis. Pedicelli fructiferi subappressi, recti, 3–5 mm longi. Siliqua anguste oblonga, glabra, subtorulosa, paucisperma, 5–6 mm longa, 1.2–1.4 mm lata. Semina oblonga, uniseriata, ca. 1.3 × 0.7 mm longa; cotyledones incumbentes.

Deep-rooted, cespitose perennial. Main roots thick, more than 15 cm long, 3–5 mm wide. Caudices short; stems decumbent, 4–6 cm long, glabrous. Basal leaves numerous, rosulate, petiolate; blades lanceolate, 2–3 cm long, 4–6 mm wide, obtuse to subacute at apex, attenuate at base, pinnatifid to sinuate or repand-dentate, pubescent with straight, simple or asymmetrically furcate trichomes 0.2–0.4 mm long; petioles persistent, erect to spreading, densely over-

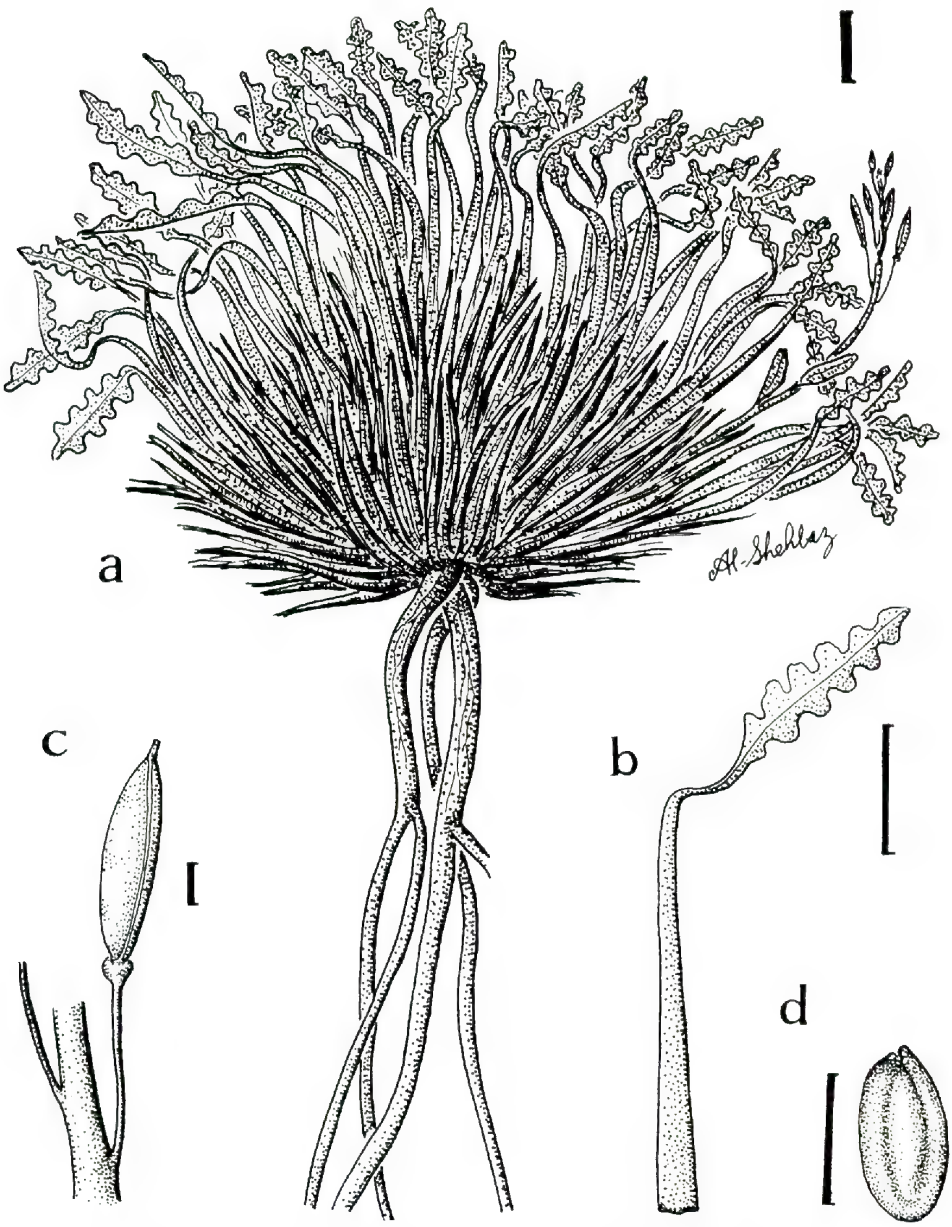


FIGURE 2. *Weberbauera densifolia* (holotype): a, plant; b, basal leaf; c, portion of infructescence with fruit; d, seed. Scale bars = 1 cm (a, b), 1 mm (c, d).

lapping, straight, 3–3.5 cm long, 2–3 mm wide, straw colored and becoming papery with age, glabrous. Cauline leaves few, petiolate; blades 8–11 mm long, 4–6 mm wide, repand to entire. Flowers not seen. Infructescences ebracteate, glabrous; fruiting pedicels erect to only slightly ascending, subappressed, straight, 3–5 mm long. Fruits narrowly oblong, subtorulose, 5–6 mm long, 1.2–1.4 mm wide, glabrous, few seeded; septa complete, membranaceous; styles 0.5–0.7

mm long. Seeds uniseriately arranged, oblong, ca. 1.3 mm long, 0.7 mm wide, obscurely reticulate; cotyledons incumbent.

TYPE. Argentina, Prov. Catamarca, Depto. Santa María, Sierra del Aconquija, 4600 m alt., 20 Feb. 1925, *S. Venturi 6610* (holotype, US (photocopy, GH)).

Weberbauera densifolia is easily distinguished from the other species of the genus by its numerous, densely overlapping leaves with persistent, straight, straw-colored petioles 3–3.5 cm long and about as long as the leaf blade. Other species of *Weberbauera* have few petioles that are much shorter than the blades and that do not form dense crowns. Furthermore, *W. densifolia* is also unique in the genus in having deeply penetrating, thick, few-branched main roots that are more than 15 cm long.

Weberbauera densifolia superficially resembles *W. spathulaefolia* in several aspects of leaf blade and fruit morphology. The two are apparently related, but such a relationship cannot be fully assessed without adequate material of the former.

3. **Weberbauera minutipila** Al-Shehbaz, sp. nov. FIGURE 3.

Herba perennis tenella, caudicibus tenuibus, caulibus decumbentibus 2–7 cm longis, sparse vel dense pubescentibus, pilis minute furcatis vel simplicibus 0.03–0.1(–0.13) mm longis. Folia basales petiolata filiformes vel anguste lineares, integra vel sparse dentata, longitudinaliter plicata vel plana (1–)2–3(–4.5) cm longa; petiolis complanatis ad basim expansis persistentibus; folia caulina ovata vel lanceolata dentato-serrata subsessilia (3–)4–8(–10) mm longa. Racemi ebracteati. Sepala erecta oblonga 1.5–2 mm longa; petala spathulata alba 2–2.7 mm longa. Pedicelli fructiferi recti subappressi 2.5–3.5(–5) mm longi. Siliqua anguste oblonga glabra subtorulosa 6–9 mm longa; stylus 0.2–0.3 mm longus. Semina uniseriata ovata 3 vel 4 in loculo.

Delicate perennial herbs. Caudices simple, slender, covered with petiolar bases of previous years. Stems decumbent to rarely ascending, simple, 2–7 cm long, sparsely to densely covered with minute, furcate or simple trichomes 0.03–0.1(–0.13) mm long, sometimes glabrescent. Basal leaves petiolate; blades filiform to narrowly linear, rarely linear-lanceolate, (1–)2–3(–4.5) cm long, 0.5–1.5(–2.5) mm wide, acute at apex, entire or rarely dentate, longitudinally plicate to flat, pubescent to glabrescent; petioles persistent, (3–)5–8(–10) mm long, flattened, conspicuously expanded at base, straw colored, glabrous. Cauline leaves short petiolate to subsessile; blades ovate to lanceolate, (3–)4–8(–10) mm long, 1.5–3.5(–5) mm wide, dentate-serrate or rarely sublaciniate. Inflorescences ebracteate racemes, slightly elongated in fruit. Sepals caducous, erect, oblong, 1.5–2 mm long, 0.7–1 mm wide, rounded at apex, nonsaccate, narrowly scarious at margin, drying lavender, glabrous or only sparsely pubescent below apex. Petals white, spatulate, 2–2.7 mm long, 1–1.2 mm wide, rounded at apex, attenuate to clawlike base. Nectar glands obscure, ringlike, subtending bases of filaments. Filaments white, erect, 1.1–1.5 mm long; anthers oblong, 0.4–0.5 mm long. Fruiting pedicels somewhat ascending, subappressed to rachis, straight, 2.5–3.5(–5) mm long, glabrous. Fruits narrowly oblong, subtorulose, 6–9 mm

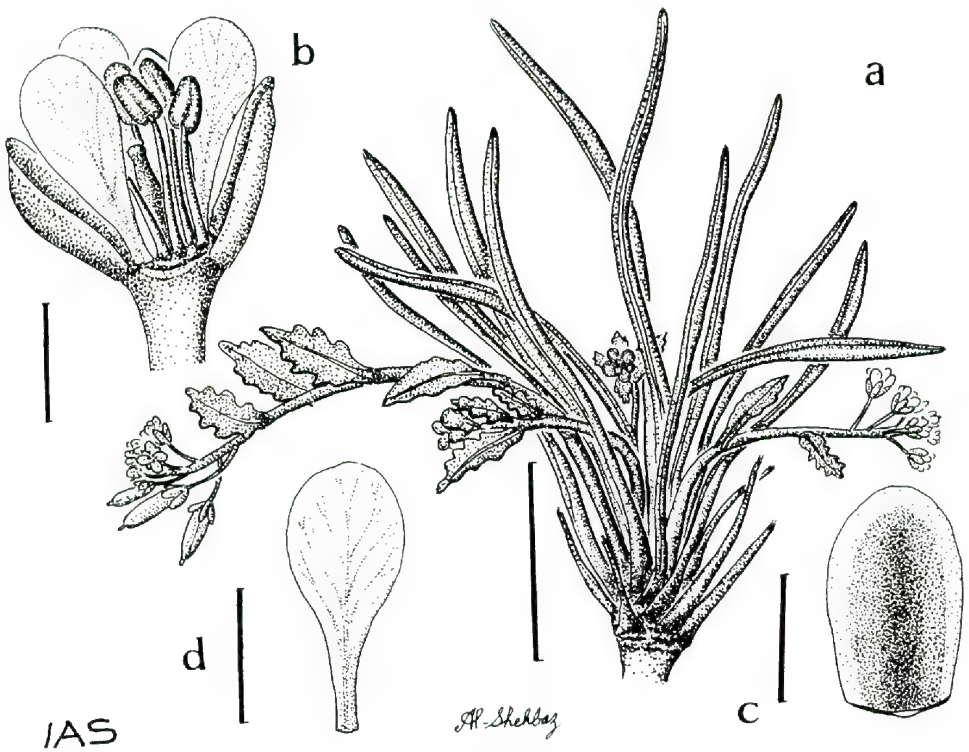


FIGURE 3. *Weberbauera minutipila* (holotype): a, plant; b, flower with 1 sepal and 1 petal removed; c, sepal; d, petal. Scale bars = 1 cm (a), 1 mm (b–d).

long, ca. 1 mm wide, glabrous; styles 0.2–0.3 mm long. Seeds 3 or 4 per locule, uniseriately arranged, ovate, ca. 1 mm long, 0.7 mm wide, brown; cotyledons incumbent; funicles slightly expanded at placental end.

TYPE. Peru, Depto. Puno, Prov. San Román, "shale barren" with rock-chip covered bare ground, on bare hills on Puno–Arequipa road at km 112.8, ca. 4 km (air) E of Tinocopalca (km 119.5), ca. 10 km W of road-turnoff to Sta. Lucía (at km 101), ca. 4000 m alt., 12 Jan. 1963, *H. H. & C. M. Iltis and D. & V. Ugent 1455* (holotype, GH; isotype, WIS).

ADDITIONAL SPECIMENS EXAMINED. **Peru.** DEPTO. AREQUIPA: Prov. Arequipa, S of Sta. Lucía on road from Puno to Arequipa, ca. 4–5 km E of Sta. Lucía, *Iltis & Ugent 1415* (WIS). **Bolivia.** DEPTO. LA PAZ: Prov. Murillo, 14 km N of La Paz, Mina Milluni, 15 km hacia Tuni Condoriri, *Beck 3832* (GH); Valle Chuquiaguillo, *Asplund 1888* (S).

Weberbauera minutipila is distinguished from the other species of the genus in having minute trichomes rarely to 0.13 mm long (see FIGURE 1c), filiform to linear basal leaves 0.5–1.5(–2.5) mm wide, usually coarsely dentate-serrate, ovate to lanceolate cauline leaves, and ebracteate inflorescences.

Both *Weberbauera minutipila* and *W. spathulaefolia* grow in Prov. Murillo, Bolivia. It is not known, however, if the two species grow sympatrically.

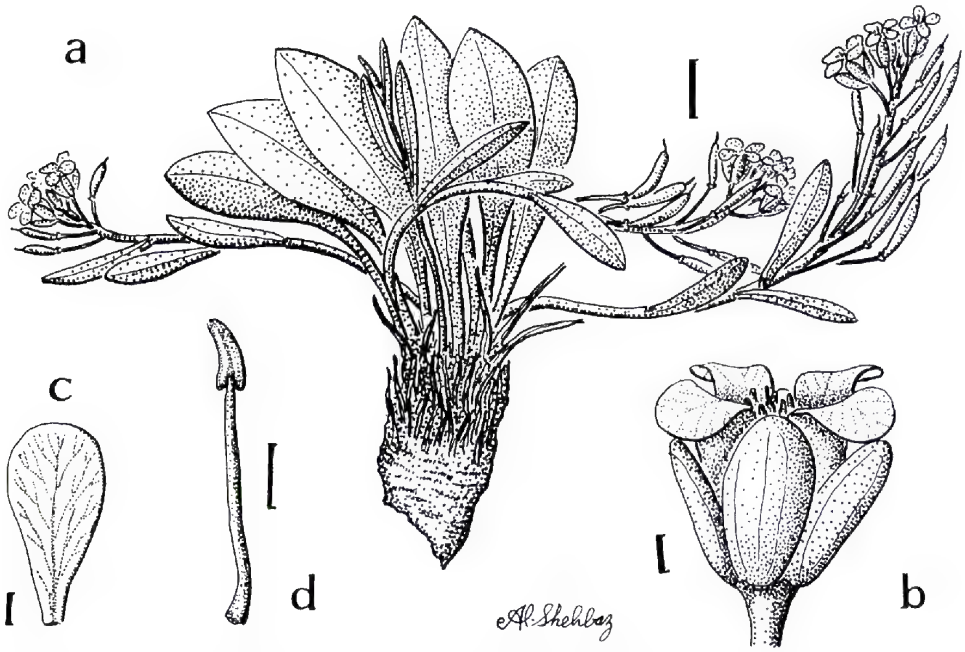


FIGURE 4. *Weberbauera smithii* (holotype): a, plant; b, flower; c, petal; d, stamen. Scale bars = 1 cm (a), 1 mm (b–d).

4. **Weberbauera smithii** Al-Shehbaz, sp. nov. FIGURE 4.

Herba glabra perennis caespitosa, caudicibus lignosis crassis 1.5–2 cm latis, caulibus decumbentibus 4–7 cm longis. Folia basales rosulata, late spathulata, succulenta, glabra, integra, apice obtusa, base attenuata, 2–4.5 cm longa, 0.6–1.3 cm lata. Racemi ebracteati. Sepala erecta, oblonga, glabra, decidua, 4.2–5.5 mm longa, 2.2–2.6 mm lata; petala alba, late spathulata, 6.5–8 mm longa, 2.8–3 mm lata. Pedicelli fructiferi, recti, 6–10 mm longi, divaricati-adscendentes. Siliqua oblonga vel linearis, obtusa 0.5–1.5 cm longa, 1.5–2 mm lata, valvis crassibus, glabris; stylus 1–1.5 mm longus. Semina matura ignota.

Perennial, glabrous, cespitose herbs with unbranched, thick, woody caudices 1.5–2 cm in diameter. Stems few, decumbent, 4–7 cm long. Basal leaves rosulate, fleshy; blades broadly spatulate, 2–4.5 cm long, 6–13 mm wide, obtuse, attenuate at base, entire, nonciliate, glabrous; petioles thick, 1–2.5 cm long. Cauline leaves subsessile; blades oblanceolate, 1–1.8 cm long, 3–5 mm wide, subacute, attenuate to broad base, entire, glabrous or with few, simple, subapical trichomes. Inflorescences ebracteate racemes, elongated in fruit. Sepals caducous, erect, oblong, 4.2–5.5 mm long, 2.2–2.6 mm wide, obtuse, nonsaccate, narrowly scarious at margin, glabrous. Petals creamy white, broadly spatulate, 6.5–8 mm long, 2.8–3 mm wide, rounded at apex, attenuate to broad, clawlike base. Nectar glands confluent, low, ringlike, subtending bases of filaments. Stamens slightly tetradynamous; filaments white, erect, slender, 3.5–4 mm long;

anthers oblong, 1–2 mm long. Fruiting pedicels divaricate-ascending, straight, 6–10 mm long. Fruits oblong to linear, 0.5–1.5 cm long, 1.5–2 mm wide, obtuse at apex, abruptly ending in style; valves thick, glabrous, with obscure midvein; styles 1–1.5 mm long. Mature seeds not seen.

Growing in cracks of exposed rocks or among rock outcrops in grasslands and margins of bare needle-ice zones at altitudes of 4770–4870 m.

TYPE. Peru, Depto. Ancash, Prov. Yungay, Huascarán National Park, Llanganuco Sector, Quebrada Ancosh at Portachuelo (77°35'W, 9°03'S), 31 Dec. 1984, *D. N. Smith & K. Goodwin 8894* (holotype, MO).

ADDITIONAL SPECIMEN EXAMINED. **Peru:** Same as type locality, *Smith 11298A* (MO).

Weberbauera smithii, named after one of it collectors, is easily distinguished from the remainder of the genus by its fleshy, glabrous leaves, thick, unbranched caudices, considerably larger flowers with petals 6.5–8 mm long, and rounded fruit apices abruptly ending in a distinct style.

Nothing can be said about the variability of this handsome species because only two plants were available for study. Field notes of the two collections above indicate that the species has purple petioles, sepals, and young fruits.

5. **Weberbauera retropila** Al-Shehbaz, sp. nov. FIGURE 5.

Herba perennis, caudicibus tenuibus ca. 2 mm latis, caulibus simplicibus adscendentes vel subdecumbentes, 2.5–5.5 cm longi. Folia basales haud rosulata, petiolata, late spathulata vel oblanceolata, dentata, 1.3–2.5 cm longa, 4–7 mm lata, sparse pubescentibus, pilis furcatis. Racemi ebracteati. Sepala erecta, oblonga, persistens, purpurea, 2–2.5 mm longa, 1–1.2 mm lata. Petala alba, spathulata, attenuata, 3–3.5 mm longa, 1–1.5 mm lata. Pedicelli fructiferi 2–3.5(–6) mm longi. Siliqua oblonga, subacuta, 5–8(–10) mm longa, 1.5–1.8 mm lata, valvis sparse pubescentibus pilis retroris simplicibus 0.1–0.25 mm longis; stylus 0.5–0.8 mm longus. Semina uniseriata ovata 1.4–1.5 mm longa.

Perennial herbs with slender rootstocks ca. 2 mm wide. Stems ascending to subdecumbent, simple, 2.5–5.5 cm long, glabrous. Basal leaves not rosulate, petiolate, caducous, often spatulate to oblanceolate, 1.3–2.5 cm long, 4–7 mm wide, dentate, sparsely pubescent with stalked, Y- or T-shaped furcate trichomes; petioles to 1 cm long. Cauline leaves similar to basal ones but smaller. Inflorescences ebracteate racemes, slightly elongated in fruit. Sepals persistent, erect, oblong, 2–2.5 mm long, 1–1.2 mm wide, obtuse at apex, membranaceous at margin, purplish, glabrous or rarely with few subapical trichomes. Petals white, spatulate, 3–3.5 mm long, 1–1.5 mm wide, attenuate to short, clawlike base. Nectar glands ringlike, poorly developed outside bases of filaments. Filaments white, erect, slender, 1.5–1.8 mm long; anthers ovate, 0.4–0.5 mm long, apiculate. Fruiting pedicels ascending, straight, 2–3.5(–6) mm long, glabrous. Fruits narrowly oblong, slightly torulose, 5–8(–10) mm long, 1.5–1.8 mm wide, subacute at apex; valves sparsely pubescent with simple, retrorse trichomes 0.1–0.25 mm long, midvein inconspicuous; septa hyaline, complete; styles 0.5–0.8 mm long; stigmas entire. Seeds usually 3 or 4 per locule, uniseriately

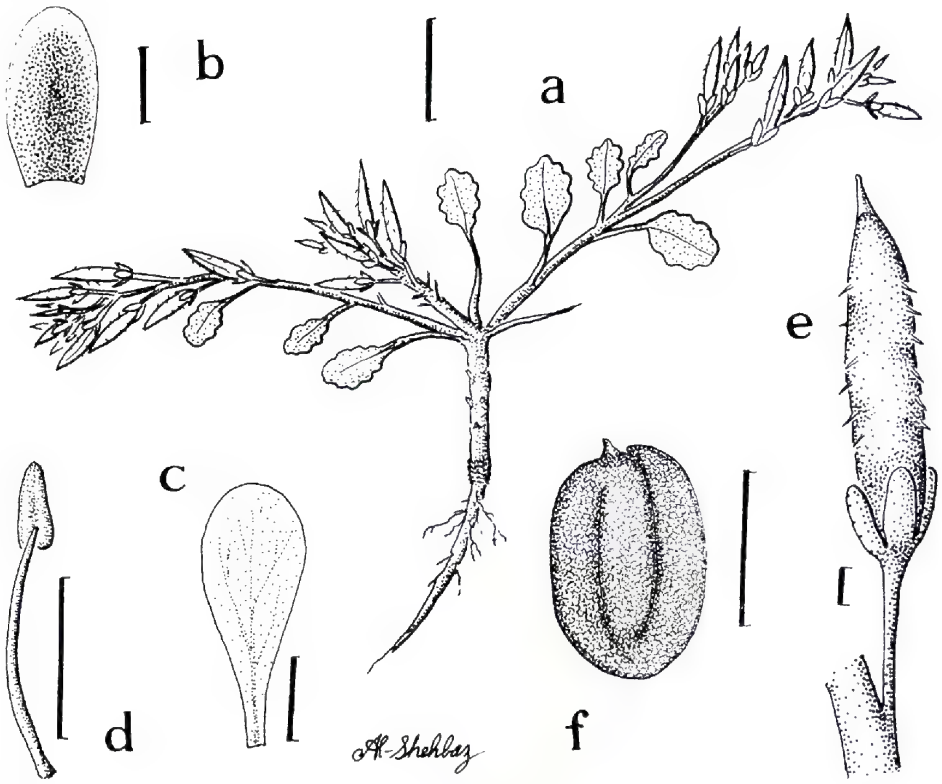


FIGURE 5. *Weberbauera retropila* (holotype): a, plant; b, sepal; c, petal; d, stamen; e, fruit and fruiting pedicel; f, seed. Scale bars = 1 cm (a), 1 mm (b–f).

arranged, ovate, 1.4–1.5 mm long, 0.9–1 mm wide, dark brown; funicles slightly expanded proximally, slender distally; cotyledons incumbent.

TYPE. Bolivia, Depto. La Paz, Prov. Pacajes, Charaña, 4000 m alt., *Asplund s.n.*, 2 March 1921 (holotype, US).

ADDITIONAL SPECIMEN EXAMINED. **Bolivia:** same as type locality, ca. 4050 m alt., *Asplund 2700* (S).

Despite the altitudinal differences between the two collections cited above, it is likely that both were made from the same population. Comparisons of Asplund's collections of several other species show that labels of his duplicates at US usually differ from those of the original set at S in only a few minor details. Therefore, the specimen above at S might well be an isotype.

Weberbauera retropila is easily distinguished in having pubescent fruits with retrorse simple trichomes, persistent calyces, slender rootstocks, fewer (three or four) seeds per locule, and sparsely pubescent leaves with Y- or T-shaped, furcate trichomes (see FIGURE 1d). Because the rootstocks are very slender and the basal leaves are caducous, the species could easily be mistaken for an annual. This aspect of habit and the presence of persistent sepals make *W. retropila*

somewhat anomalous in the genus. However, all other features of the species are characteristic of *Weberbauera*.

6. **Weberbauera herzogii** (O. E. Schulz) Al-Shehbaz, comb. nov.

Sarcodraba herzogii O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem **10:** 563. 1929. TYPE: Bolivia, auf erde zwischen Felsplatten der Hügel über dem Titicacasee bei Guaqui, ca. 3900 m, *T. Herzog 2510* (holotype, B! (photos, F!, GH!, MO!, NY!); isotypes, G! (photos, F!, MO!), Z!).

Caudices slender, simple or rarely few branched. Stems decumbent to erect, unbranched, (1.5–)3–12 cm long, hirsute with spreading to reflexed simple trichomes 0.4–1 mm long, rarely glabrous or glabrescent. Basal leaves petiolate; blades broadly obovate to spatulate, (1–)1.5–3.5 cm long, (4–)5–10 mm wide, rounded at apex, entire to repand or rarely dentate, usually ciliate; petioles ciliate, (0.5–)0.7–2 cm long. Cauline leaves 0.3–1.1(–2) cm long, 2–5(–10) mm wide, dentate to repand or entire. Inflorescences bracteate racemes, elongated or rarely unexpanded in fruit; bracts 3-toothed to entire. Sepals caducous, oblong to ovate, (2.2–)3–4 mm long, 1.5–2 mm wide, obtuse, scarious at margin, glabrous to sparsely hirsute. Petals white to lavender, spatulate to broadly obovate, 3.5–5(–7) mm long, 1.5–2.5 mm wide. Filaments white, erect, slender, 2.2–4 mm long; anthers oblong, 0.6–0.9 mm long. Fruiting pedicels ascending to divaricate, usually straight, (3–)4–10 mm long. Fruits linear to oblong, terete, nontorulose, (5–)8–18 mm long, 1.6–2.1 mm wide, usually attenuate to slender style; valves glabrous, with prominent to obscure midvein; septa hyaline; styles slender, (0.8–)1.2–2.5 mm long; receptacles 4-angled, usually expanded. Seeds uniseriately arranged, oblong, 1.5–1.8 mm long, 0.8–1 mm wide, light brown; funicles strongly differentiated into broad, persistent base and filiform distal portion.

Flowering early December through February; growing at altitudes of 3125–4700 m.

REPRESENTATIVE SPECIMENS EXAMINED. **Argentina.** PROV. JUJUY: Depto. Humahuaca, Esquinas Blancas, between Tres Cruces and Humahuaca, *Ruthsatz 13/18* (GH). **Bolivia.** DEPTO. LA PAZ: 5 km E of Villa Santa Fe (ca. 100 km N of Oruro), *Conrad 2692* (MO); 2 km W of Villa Santa Fe, *Conrad 2709* (MO); Prov. Ingavi, Guaqui, *Asplund 2226* (S). DEPTO. POTOSÍ: Orocoro, near Ventilla, *Ceballos, Charpin, Fernández Casas, & Valdés-Bermejo 252* (G); Potosí, *Cárdenas 173* (GH), *399* (US); Miraflos, *D'Orbigny 1347* (P). **Peru.** Depto. Puno, Puno, *Shepard 38* (GH, US), *Soukup 106* (F); Santa Lucía, *Sharpe 143* (F); without further locality, *Gay 2256* (P).

Weberbauera herzogii, which is often confused with *W. spathulaefolia,* is easily distinguished by its ciliate basal leaves, exclusively simple trichomes, inflorescences bracteate along their entire length, large (1.5–1.8 mm) seeds, and attenuate fruits that terminate in slender styles (0.8–)1.2–2.5 mm long. The closely related *W. spathulaefolia* has nonciliate leaves, furcate trichomes sometimes mixed with simple ones (or the plant is glabrous), ebracteate or partially bracteate (rarely completely bracteate) inflorescences, smaller ((0.8–)1–1.4 mm long) seeds, and usually blunt fruits with styles almost always less than 1 mm long.

Both *Weberbauera herzogii* and *W. spathulaefolia* grow in Depto. Potosí, Bolivia. *Cárdenas 399,* cited under the former species, and *Cárdenas 398,* cited under the latter, were probably collected from the same general area. It is not known, however, if the two species are actually sympatric.

In a few collections (e.g., *Cárdenas 173, 399*) the rachises of the central infructescences do not elongate, and the fruits appear as if borne on short scapes. However, this abnormality is insignificant because it is found within certain collections (e.g., *Ceballos et al. 252*) that otherwise have normal infructescences.

The placement of *Weberbauera herzogii* in *Sarcodraba* by Schulz (1929) was not based on a careful evaluation of the boundaries of these genera. Schulz (1924, 1936) stated that *Sarcodraba* differs from *Weberbauera* mainly in having silicles instead of siliques. Apparently, he did not examine any fruiting material of *W. herzogii.* The species is so closely related to *W. spathulaefolia* that the two have probably evolved from a common ancestor.

7. **Weberbauera bracteata** (O. E. Schulz) J. F. Macbr. Candollea **5:** 356. 1934.

Pelagatia bracteata O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 192. 1924. TYPE: Peru, Depto. Ancash, Prov. Pallasca, Cordillera of Pelagatos, 4600 m alt., 23 Jan. 1920, *A. Weberbauer 7234* (holotype, B! (photos, F!, GH!, MO!, NY!); isotypes, F(2 sheets)!, G!).

Small, cespitose perennials. Caudices simple, thick, 6–12 mm wide. Stems decumbent, 3–6 cm long, glabrous. Basal leaves rosulate, petiolate; blades oblanceolate to spatulate, 1.5–4 cm long, 4–9 mm wide, lyrate-pinnatifid, with 2 to 4 lateral lobes, rarely repand or entire, ciliate with simple, straight trichomes 0.3–0.9 mm long, glabrous on both surfaces or sometimes pubescent on upper. Cauline leaves petiolate; blades obovate to spatulate, 7–13 mm long, 2–4.5 mm wide, gradually reduced in size upward, rounded at apex, entire or rarely repand, ciliate. Inflorescences corymbose racemes, bracteate throughout, elongated in fruit. Sepals caducous, erect, oblong to ovate, 1.5–2.2 mm long, 1–1.1 mm wide, rounded at apex, nonsaccate at base, membranaceous at margin, glabrous. Petals white, spatulate, 2.5–3 mm long, to 1 mm wide, rounded at apex, attenuate to clawlike base. Filaments white, erect, 1.5–2 mm long; anthers oblong, 0.6–0.7 mm long. Fruiting pedicels 3–7 mm long. Fruits ascending, oblong, terete, straight, nontorulose, 6–9 mm long, 1.5–2 mm wide, obtuse at apex; valves glabrous, with conspicuous midvein; styles to 0.2 mm long. Seeds 3 to 5 per locule, uniseriately arranged, oblong, 1.4–1.6 mm long, 0.6–0.7 mm wide, brown; funicles broad at proximal end.

Weberbauera bracteata is known only from the type collection. It is most closely related to *W. herzogii,* from which it is distinguished in having glabrous stems, lyrately pinnatifid basal leaves, small petals to 3 mm long, obtuse fruits, and minute styles to 0.2 mm long. *Weberbauera herzogii* usually has retrorsely pubescent stems, entire to dentate basal leaves, larger (3.5–5(–7) mm long) petals, attenuate fruits, and conspicuous styles (0.8–)1.2–2.5 mm long. The differences between *W. bracteata* and the closely related *W. cymosa* are given under the latter.

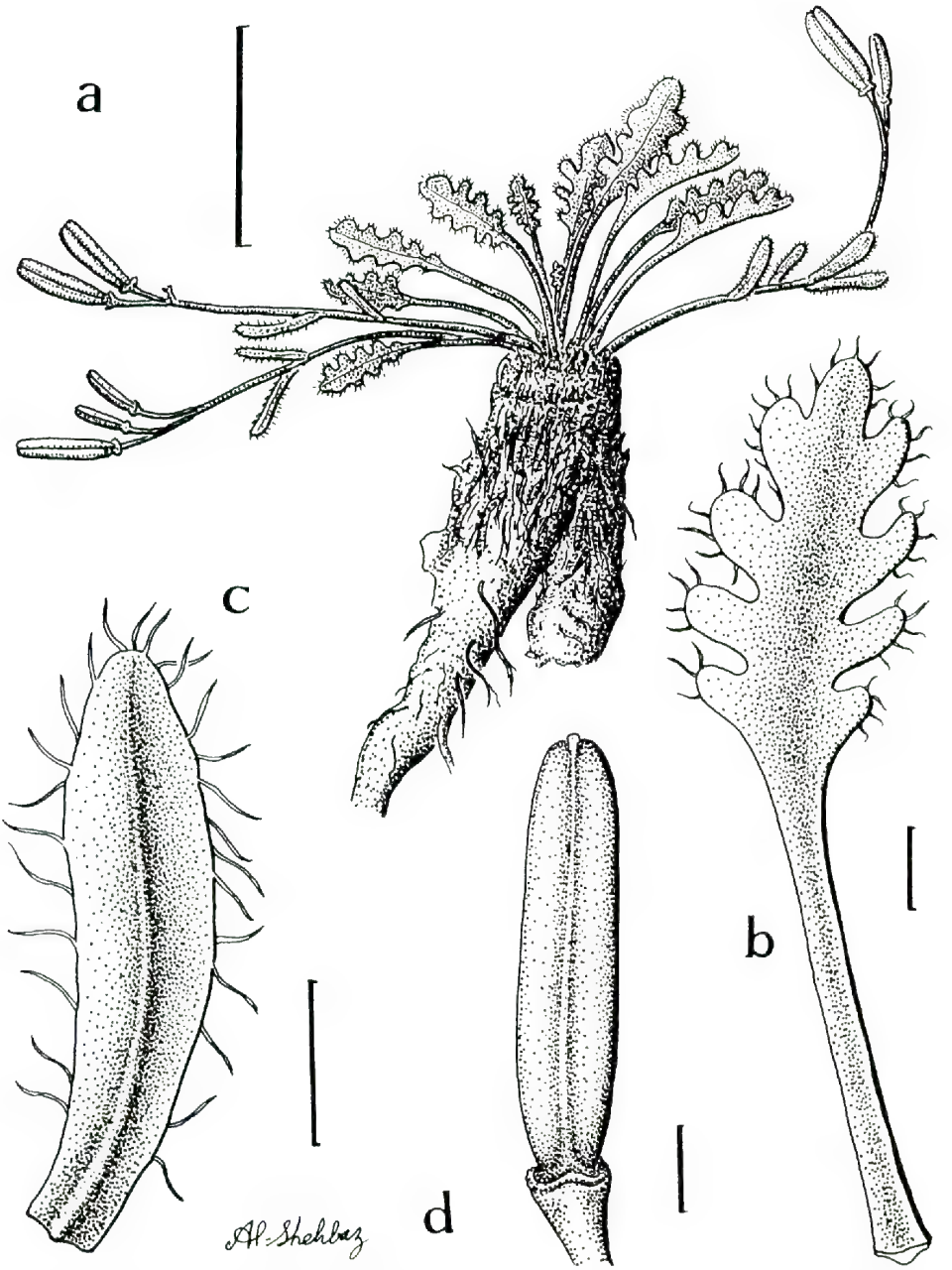


FIGURE 6. *Weberbauera cymosa*: a, plant; b, basal leaf; c, cauline leaf; d, fruit. Scale bars = 1 cm (a), 1 mm (b–d).

As indicated above, Schulz's (1924, 1936) placement of *Weberbauera bracteata* in the monotypic *Pelagatia* is not supported by any morphological evidence. His allegation (1924; see key, p. 181) that *Pelagatia* differs from *Weberbauera* in having flattened instead of slender funicles is erroneous because

almost all plants that I have examined of *W. spathulaefolia,* the generic type, have flattened funicles.

8. **Weberbauera cymosa** Al-Shehbaz, sp. nov. FIGURE 6.

Herba caespitosa perennis tenella, caudicibus crassis, caulibus decumbentibus, glabris, tenuibus, 1–1.7 cm longis. Folia basales petiolata, pinnatifida, rosulata, 5–15 mm longa, 2–3 mm lata, lobis lateralibus 3- vel 5-jugis, oblongis vel ovatis, ciliatis, 0.8–1.2 mm longis, 0.4–0.6 mm latis; folia caulina anguste oblonga, sessiles, ciliata, integra, 2.5–4 mm longa. Inflorescentia ebracteata, 2- vel 3-floribus, dichasialium plus minusve faciens. Sepala oblonga, erecta, nonsaccata, glabra, 1.4–1.6 mm longa. Petala alba, spathulata, ca. 1.4 mm longa. Pedicelli fructiferi recti 2.5–5 mm longi. Siliqua oblonga, obtusa, glabra, 4–5.5 mm longa; stylus obsoletus usque ad 0.3 mm longus. Semina immatura uniseriata, ovata, ca. 1.2 × 0.7 mm, funiculis filiformibus.

Small, cespitose perennials. Caudices simple, thick, 4–6 mm wide. Stems decumbent, slender, 1–1.7 cm long, glabrous. Basal leaves rosulate, petiolate; blades ovate to lanceolate, 5–15 mm long, 2–3 mm wide, pinnatifid, the lateral lobes in 3 to 5 pairs, oblong to ovate, 0.8–1.2 mm long, 0.4–0.6 mm wide, obtuse, ciliate with simple trichomes 0.3–0.5 mm long; petioles 3–8 mm long, glabrous. Cauline leaves few, sessile; blades narrowly oblong, 2.5–4 mm long, 0.8–1.3 mm wide, obtuse to rounded, entire, ciliate. Inflorescences ebracteate, highly modified, dichasiumlike or 2- or 1-flowered racemes. Sepals erect, oblong, 1.4–1.6 mm long, ca. 0.7 mm wide, rounded at apex, glabrous. Petals white, spatulate, ca. 1.4 mm long. Filaments erect, ca. 1.3 mm long; anthers oblong, 0.3–0.4 mm long. Fruiting pedicels straight, 2.5–5 mm long. Fruits oblong, terete, 4–5.5 mm long, ca. 1.5 mm wide, obtuse at apex, glabrous; styles obsolete to 0.3 mm long; stigmas entire. Seeds (immature) 4 or 5 per locule, uniseriately arranged, ovate, ca. 1.2 mm long, 0.7 mm wide, brown; funicles filiform.

TYPE: Bolivia, Depto. La Paz, Murillo, near Palca, base of Illimani, 4800–5000 m alt., 25 Feb. 1979, *A. Ceballos, A. Charpin, J. Fernández Casas, & E. Valdés-Bermejo 543* (holotype, G).

Weberbauera cymosa is known only from the type collection. It is most closely related to *W. bracteata,* which it resembles in having ciliate, pinnatifid, rosulate basal leaves, ciliate, entire cauline leaves, oblong fruits with minute styles, and few, uniseriately arranged seeds. However, it is easily distinguished by its ebracteate, two- or three-flowered, cymelike, modified racemes, sessile cauline leaves, and smaller basal leaves. *Weberbauera bracteata* has bracteate racemes, petiolate cauline leaves, and larger basal leaves.

Weberbauera cymosa resembles *W. trichocarpa* in having highly modified, cymelike racemes, but the two appear to have little else in common. In fact, *W. cymosa* is probably a sister species of *W. bracteata,* whereas *W. trichocarpa* is closer to *W. spathulaefolia* than to any other species of the genus. It is most likely, therefore, that cymelike racemes evolved independently in those two species of *Weberbauera.*

9. **Weberbauera trichocarpa** (Muschler) J. F. Macbr. Candollea **5:** 356. 1934.

Eudema trichocarpum Muschler, Bot. Jahrb. Syst. **40:** 276. 1908. *Brayopsis trichocarpa* (Muschler) Gilg & Muschler, Bot. Jahrb. Syst. **42:** 484. 1909. *Alpaminia trichocarpa* (Muschler) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 191. 1924. TYPE: Peru, above Lima, near Alpamina (as Alpamia in the original publication), 4500 m alt., 2 March 1904, *A. Weberbauer 5119* (holotype, B!).

Small, cespitose perennials, densely covered throughout with appressed, sessile, malpighiaceous trichomes 0.5–1.1 mm long, these oriented parallel to long axes of organs they cover. Caudices simple or branched, slender, usually covered with petiolar remains of previous years. Stems decumbent, rarely ascending or procumbent, unbranched, terete, (1–)2–4.5(–6) cm long. Basal leaves petiolate; blades linear to linear-lanceolate, (1–)2–4(–4.5) cm long, (1.5–)2–3.5 mm wide, acute, attenuate at base, entire, conduplicate or rarely flat, densely pubescent on both surfaces; petioles persistent, flattened, 5–10(–13) mm long, to 4 mm wide at base, somewhat membranaceous at margin. Cauline leaves short petiolate; blades ovate to lanceolate, 5–9(–11) mm long, 1.5–3(–3.5) mm wide, entire. Inflorescences cymelike, umbellate, usually 3-flowered racemes, often subtended at base by leafy bracts. Sepals caducous to persistent, erect, oblong, 3.5–4 mm long, 1.5–2 mm wide, obtuse at apex, nonsaccate, narrowly scarious at margin, densely pubescent on outside. Petals pink to pinkish-yellow, spatulate, 5–6.5 mm long, 1.5–2.2 mm wide, rounded at apex, attenuate to pubescent claw. Filaments white, erect, 3–4 mm long; anthers narrowly oblong, 0.8–1.1 mm long, minutely apiculate. Fruiting pedicels straight, (6–)7–15(–17) mm long, densely pubescent. Fruits oblong to linear, terete, straight, 7–13(–15) mm long, 1.7–2.4(–2.6) mm wide, obtuse at both ends; valves densely pubescent, with obscure midvein; septa hyaline; styles (0.4–)0.6–0.8(–1) mm long, glabrous. Seeds numerous, biseriately arranged in each locule, oblong to ovate, 1–1.2 mm long, 0.6–0.7 mm wide, light to dark brown; funicles flattened proximally, filiform distally.

Endemic to Peru, where it grows on limestone slopes and cliffs at altitudes of 4200–4800 m.

REPRESENTATIVE SPECIMENS EXAMINED. **Peru.** DEPTO. ANCASH: Prov. Pallasca, Conchucós, *Weberbauer 7229* (B, F, GH), *7229a* (F, GH). DEPTO. LIMA: Río Blanco, *Macbride 2990* (F, GH, MO, NY, US). DEPTO. PASCO: Cerro de Pasco, *Asplund 11778* (S), *11835* (S), *Macbride 3073* (CAS, F, GH, MO, NY, US).

Weberbauera trichocarpa is readily distinguished from the other species of the genus by its dense covering of appressed, sessile, malpighiaceous trichomes on almost all parts of the plant (including sepals, outer portion of claws, and fruit valves) (see FIGURE 1a) and by its cymelike inflorescences. Submalpighiaceous trichomes are found on stems of *W. spathulaefolia*; cymelike racemes also characterize *W. cymosa,* and pubescent fruits occur in *W. retropila.* The presence of pubescent claws is restricted to *W. trichocarpa.* However, this character alone does not justify the separation of the species to a distinct genus, and some genera (e.g., *Sisymbrium*) of the Brassicaceae include species with glabrous petal claws and others with pubescent ones.

Perhaps the most remarkable feature of *Weberbauera trichocarpa* and *W. cymosa* is the cymelike, modified raceme. To my knowledge, no other species of the Brassicaceae has this inflorescence type. The flowers and fruits in *W. trichocarpa* are typically arranged in threes, with one generally terminating the stem. Of the 216 inflorescences studied, this "dichasiumlike" raceme was observed in 112 (ca. 52 percent). Two-flowered inflorescences were found in 88 (ca. 41 percent) of the total, and most of these have a third abortive flower. Therefore, the basic inflorescence type for the species is a three-flowered raceme. One-, four-, and five-flowered inflorescences constitute the remaining seven percent. Variation in the number of flowers could be observed on various stems of a given plant. An example is found in *Macbride 2990* (MO).

10. **Weberbauera colchaguensis** (Barnéoud) Al-Shehbaz, comb. nov.

Cardamine? colchaguensis Barnéoud *in* C. Gay, Fl. Chile **1:** 115. 1846. *Sisymbrium colchaguensis* (Barnéoud) Wedd. ex Fourn. Rech. Anat. Tax. Fam. Crucif. (Thesis, Paris), 134. 1865. *Hesperis colchaguensis* (Barnéoud) Kuntze, Revis. Gen. Pl. **2:** 934. 1891. *Stenodraba colchaguensis* (Barnéoud) O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem **11:** 644. 1932. TYPE: Chile, [Región VII, Del Libertador General Bernardo O'Higgins,] Colchagua, cordillera del Cajón del Azufre, cerca del volcán de Talcarégue, 8000–9000 ft [ca. 2438–2743 m] alt., *Gay 171* (holotype, P, not seen; isotypes?, G(2 sheets)!).

Erysimum? pusillum Gillies ex Hooker & Arn. Bot. Misc. **3:** 140. 1833, non *E. pusillum* Bory & Chaub. *in* Bory, Exp. Sci. Morée, Bot. **3**(2): 190. 1832. *Braya pusilla* A. Gray, U. S. Expl. Exped. Phan. **15**(1): 57. 1854. *Sisymbrium pusillum* Wedd. ex Fourn. Rech. Anat. Tax. Fam. Crucif. (Thesis, Paris), 131. 1865, non *S. pusillum* Villars, Fl. Delph. *in* Gilib. Syst. Pl. Europ. **1:** 69. 1785. *Hesperis pusilla* Kuntze, Revis. Gen. Pl. **2:** 935. 1891. *Weberbauera pusilla* O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 194. 1924. *Stenodraba pusilla* Boelcke, Dansk. Bot. Ark. **22:** 143. 1968. TYPE: Chile, el Cerro de la Porcura and la Cumbre de los Andes, 12,000 ft [ca. 3656 m] alt., *Gillies 8* (holotype, E! (photo, A!)).

Draba andina Philippi, Linnaea **28:** 669. 1856. *Stenodraba andina* (Philippi) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 187. 1924. TYPE: Chile, [Región VIII, Maule,] "in andibus prope oppidum Linares legit Germain" (holotype, SGO, not seen).

Draba patagonica Philippi, Linnaea **28:** 669. 1856. *Stenodraba andina* (Philippi) O. E. Schulz var. *patagonica* (Philippi) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 188. 1924. *Stenodraba patagonica* (Philippi) Ravenna, Nordic J. Bot. **1:** 141. 1981. *Stenodraba pusilla* Boelcke var. *patagonica* (Philippi) Boelcke, Fl. Patagonica **4a:** 530. 1984. TYPE: Chile, [Región XI, Los Lagos,] Volcani de Osorno, *Philippi s.n.,* March 1852 (holotype, SGO, not seen).

Arabis drabaeformis Schldl. Flora **39:** 410. 1856. TYPE: Chile, [Región X, Araucanía,] Cordillera de Ranco, *Lechler 2958* (holotype, HAL; isotypes, G!, P!).

Stenodraba andina (Philippi) O. E. Schulz var. *hirticaulis* O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 188. 1924. TYPE: Chile, "Gipfel des Berges Pichiguan," 1852, *Philippi 67* (holotype, B!).

Stenodraba andina (Philippi) O. E. Schulz var. *stylosa* O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 188. 1924. TYPE: Chile, [Región X, Araucanía,] Volcán Lanín, 1800 m alt., *Neger s.n.,* April 1897 (holotype, B; isotypes, M(2 sheets)!).

Cespitose perennials. Caudices much branched, slender, the branches terminated in rosettes and covered at base with petioles of previous years. Stems subdecumbent to ascending or erect, simple or rarely branched, (1.5–)3–13(–

22) cm long, glabrous or pubescent with simple and/or rarely furcate trichomes. Basal leaves rosulate, short to long petiolate; blades oblanceolate to spatulate or obovate, rarely oblong, (5–)7–22(–25) mm long, 2–4.5(–6) mm wide, rounded at apex, cuneate to attenuate at base; entire to repand or dentate, rarely sinuately lobed, conspicuously ciliate with simple trichomes 0.6–1 mm long; petioles persistent, to 10 mm long, ciliate. Cauline leaves few, sessile; blades oblong to elliptic or obovate, (2–)4–8 mm long, 1–2.5 mm wide, ciliate and often densely pubescent with simple trichomes. Inflorescences ebracteate, corymbose racemes, rarely lowermost flowers bracteate; infructescences subumbellate or rarely elongated and to 4 cm long; rachises glabrous or pubescent. Sepals caducous, erect, oblong, 1.7–2.5 mm long, scarious at margin, glabrous to hispid. Petals white, sometimes with purplish patch on back, oblong-oblanceolate, 2–3.5 mm long, rounded at apex. Filaments 1.4–1.5 mm long; anthers 0.3–0.8 mm long. Fruiting pedicels erect and subappressed to rachis, very rarely divaricate-ascending, stout, straight, 1.5–4.5(–7) mm long, glabrous to pubescent. Fruits subsessile, oblong to linear, (4–)5–10(–13) mm long, 1.4–2(–2.2) mm wide; valves smooth, glabrous, with prominent midvein; septa hyaline; styles obsolete to 0.2(–0.6) mm long. Seeds 3 to 6 per locule, uniseriately to somewhat biseriately arranged, oblong to ovate, 1.1–1.4(–1.6) mm long, 0.6–0.8(–1) mm wide, dark brown; funicles slender throughout or somewhat expanded at placental end.

Growing on stony hillsides at altitudes of 900–3350 m.

REPRESENTATIVE SPECIMENS EXAMINED. **Argentina.** PROV. MENDOZA, Atuel Valley: near road to Volcán Orero, *Böcher, Hjerting, & Rahn 1872* (C); Laguna Atuel, *Böcher, Hjerting, & Rahn 1976* (C, MO); El Angulo, *Hjerting, Petersen, & Rahn 452* (C), *Böcher, Hjerting, & Rahn 1911* (C); Piedra del Burrero, Val Tordilla, *Wilczek 425* (G, 2 sheets); Cajón del Burro, *Wilczek 439* (G, US). PROV. NEUQUÉN: Pino Hachado, *Hauman s.n.*, Feb. 1920 (BA); Los Lagos, Filo Machete al Co. Rothleugal, *Dierre 929* (LIL). PROV. RÍO NEGRO: Cordón del Río Colorado, Cerro Gorra, *Moreau s.n.*, 19 Feb. 1940 (BA, 2 sheets); Cerro Dormilón, *Moreau s.n.*, 2 Feb. 1940 (BA); Parque Nac. Nahuel Huapi [PNNH], Cerro Rigi, *Pedersen 1599* (C), *Moreau s.n.*, 23 Jan. 1940, Feb. 1945 (BA, 3 sheets); PNNH, Co. Catedral, *Moreau s.n.*, 4 March 1943 (BA, 2 sheets); PNNH, Hito Mirador, *Moreau s.n.*, 19 Feb. 1943 (BA); PNNH, Hito Millaqueo, *Moreau s.n.*, 20 Feb. 1943 (BA). **Chile.** [REGIÓN IV, COQUIMBO:] PROV. Choapa, La Vega Redonda, E of La Vega Escondida, *Morrison 16995* (DS, UC). [REGIÓN VII, DEL LIBERTADOR GENERAL BERNARDO O'HIGGINS:] PROV. Colchaqua, Las Damas, *Philippi 91b* (SGO); Valle Hermoso, *Philippi 91a* (SGO). [REGIÓN VIII, MAULE:] PROV. Curicó, El Valle de los Ciegos, near the volcano of Peteroa, *Bridges 1120* (BM, 2 sheets; E); PROV. Talca, Cordillera de Talca, *Philippi 91c* (SGO); PROV. Linares, Cordillera de Maule, *Germain s.n.*, 1856 & 1857 (BM; G, 2 sheets); Linares, *Philippi s.n.*, 1876 (B, F, G). [REGIÓN X, ARAUCANÍA:] PROV. Cautín, Villarrica, *Neger s.n.*, 1897 (M). [REGIÓN XI, LOS LAGOS:] PROV. Osorno, Paso Puyehue, *Sparre & Constance 10812* (UC). REGIÓN XII: Cerro Agudo, *Arroyo & Squeo 870116* (CONC).

Schulz (1924) misinterpreted the limits of *Weberbauera colchaguensis* (as *pusilla*), because except for the type, all his other citations belong to *W. spathulaefolia*. The type collection, however, is conspecific with the plants that Schulz recognized first (1924) as *Stenodraba andina* and later (1932) as *S. colcha-*

guensis. Boelcke (1968) was the first to reduce the last two names to the synonymy of *S. pusilla,* but as is shown below, he maintained *Stenodraba* as a distinct genus.

When published, *Erysimum pusillum* Gillies ex Hooker & Arn. was a later homonym of *E. pusillum* Bory & Chaub. According to Stafleu & Cowan (1976, 1979), the first and second homonyms were published in March 1833 and September 1832, respectively. Therefore, all combinations based on the former, including *Weberbauera pusilla* (Gillies ex Hooker & Arn.) O. E. Schulz, are illegitimate and should be treated as new names based on the type of *Erysimum pusillum* Gillies ex Hooker & Arn., rather than as new combinations (see ICBN, Article 72). The earliest legitimate name for the species is *Cardamine colchaguensis* Barnéoud, and therefore a new combination based on that name is needed in *Weberbauera.* Unaware of the fact that Gillies' name was a later homonym, Boelcke (1968) proposed the combination *Stenodraba pusilla* (Gillies ex Hooker & Arn.) Boelcke, but this name is illegitimate, and the species should be known in *Stenodraba* as *S. colchaguensis* (Barnéoud) O. E. Schulz.

Weberbauera colchaguensis is variable in shape and margin of basal leaves, length of infructescences, pubescence of stems and leaves, and length and width of fruits. Plants with pubescent stems were recognized by Schulz (1924) as var. *hirticaulis,* and those with dentate leaves were treated as var. *patagonica* (as *Stenodraba andina*). However, plants with glabrescent or densely pubescent stems are found within the same population, while dentate and entire leaves are often found on the same plant. In my opinion, none of the numerous variants of the species deserves formal recognition because the variation usually occurs within populations and does not correlate with geography. The species has been reported to grow as far south into Patagonia as Prov. Santa Cruz. Although I have not seen any material from that area, I have used Boelcke's (1984) work as the basis for mapping the five southernmost localities of the species (see MAP 2).

Ravenna (1981, p. 141) argued that *Stenodraba andina* var. *patagonica* should be recognized as a distinct species, *S. patagonica* (Philippi) Ravenna, because it differs from *S. andina* in the "larger size of all parts of the plant," as well as in having "less flattened and more obtuse pods." These alleged differences are unrealistic, and *Weberbaurea colchaguensis* shows continuous variation in most parts, particularly the fruits. Boelcke (1984) reduced *S. patagonica* to a variety of *S. pusilla,* but his new combination was illegitimate for two reasons. First, he chose the illegitimate name *S. pusilla* instead of *S. colchaguensis* for the species. Second, his new combination was invalidly published because the basionym (*Draba patagonica* Philippi) and a full and direct reference to its author and place of valid publication were not given (see ICBN, Article 33.2).

Weberbauera colchaguensis is distinguished by its slender, much-branched caudex, ciliate leaves, inconspicuous flowers with petals less than 3 mm long, subumbellate infructescences, stout fruiting pedicels usually less than 5 mm long, and short styles rarely to 0.6 mm. It is most closely related to *W. stenophylla* and *W. chillanensis,* from which it is distinguished by features listed under the latter species.

11. **Weberbauera chillanensis** (Philippi) Al-Shehbaz, comb. nov.

Draba chillanensis Philippi, Anales Univ. Chile **2**: 377. 1862. *Stenodraba chillanensis* (Philippi) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 188. 1924. TYPE: Chile, [Región IX, Biobío; Prov. Ñuble,] Termas de Chillán, *Philippi s.n.* (SGO *49187* (photo, UC!)).
Stenodraba chillanensis (Philippi) O. E. Schulz f. *laxa* O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 189. 1924. TYPE: Chile, [Región IX, Biobío,] valley of Nieblas, Termas de Chillán, *Philippi s.n.*, Jan. 1877 (as 1887) (B!, SGO!).

Cespitose perennials. Caudices multibranched, the branches slender, terminated in rosettes, covered with petiolar remains of previous years. Stems subdecumbent to ascending, (3–)6–14(–20) cm long, glabrous. Basal leaves rosulate, petiolate; blades spatulate to oblanceolate, sometimes linear-lanceolate, (5–)14–30(–40) mm long, (1–)2–3.5(–6) mm wide, obtuse to subacute at apex, attenuate at base, dentate, ciliate with simple and/or long-stalked furcate trichomes to 1 mm long. Cauline leaves few, linear-lanceolate, 7–15(–30) mm long, 1–1.5 mm wide, entire, ciliate. Inflorescences ebracteate, corymbose racemes, elongated in fruit. Sepals spreading, oblong to ovate, 2–2.6(–3) mm long, 1.2–1.5 mm wide, scarious at margin, glabrous or sparsely pubescent. Petals white, drying purplish in center, oblanceolate to spatulate, 2.5–3.5 mm long, 1.2–1.5 mm wide, rounded at apex, attenuate to clawlike base. Filaments somewhat spreading, 2.2–3 mm long; anthers oblong, 0.7–0.8 mm long. Fruiting pedicels divaricate-ascending, straight, (4–)6–11(–18) mm long, glabrous. Fruits divaricate-ascending, linear, flattened parallel to septum, nontorulose, straight, 9–19(–22) mm long, 1.5–1.8(–2.2) mm wide; valves glabrous, with prominent midvein; styles slender, 0.5–0.9(–1.1) mm long. Seeds uniseriately arranged in each locule, oblong, 1.4–1.6 mm long, 0.7–0.9(–1) mm wide, dark reddish-brown; funicles thickened at placental end.

REPRESENTATIVE SPECIMENS EXAMINED. **Argentina.** PROV. MENDOZA: Depto. Malargüe, Baños del Azufre, *Castellanos s.n.*, 19 Jan. 1941 (BA). **Chile.** [REGIÓN VIII, MAULE:] Prov. Curicó, Cajón del Azufre, *Albert s.n.*, Feb. 1891 (SGO); Cordillera Curicó, *Reiche s.n.* (B, CONC); Baños, *Vidal s.n.* (SGO); Volcán Peteroa, *Werdermann 604* (B, BM, E, F, G, GH, M, MO, NY, U, UC, Z); Prov. Talca, Cordillera Talca, Laguna de aguas calientes, *Philippi 1615a* (SGO); Prov. Linares, Thermae Longavi, *Schönemann 2277* (SGO). [REGIÓN IX, BIOBÍO:] Prov. Ñuble, Cordillera de Chillán, Termas de Chillán, *Jaffuel 3722* (GH), *Philippi s.n.*, Feb. 1892 (SGO).

Weberbauera chillanensis is closely related to *W. colchaguensis* and *W. stenophylla*. All three have narrowly spatulate to oblanceolate, ciliate basal leaves, slender caudex branches each terminated by a rosette, persistent petioles, and ebracteate inflorescences. *Weberbauera stenophylla* is easily distinguished by its entire basal leaves, elongate infructescences, large petals (3.5–)4–5 mm long, and styles 1.5–2 mm long. Both *W. chillanensis* and *W. colchaguensis* usually have dentate leaves, shorter petals (to 3.5 mm), and stout or slender styles rarely reaching 1 mm in length. *Weberbauera chillanensis* is separated from *W. colchaguensis* in having conspicuously flattened fruits 9–19(–22) mm long, slender, divaricate-ascending fruiting pedicels usually more than 6 mm long, elongate infructescences, and slender styles 0.5–0.9(–1.1) mm long. In contrast, *W. colchaguensis* has subterete or slightly flattened fruits (4–)5–10(–13) mm

long, stout, erect fruiting pedicels almost always less than 6 mm, usually subumbellate infructescences, and obsolete or stout styles rarely to 0.6 mm. Furthermore, the occurrence of furcate trichomes on the leaves of *W. chillanensis* and their absence in *W. colchaguensis* and *W. stenophylla* is a useful diagnostic feature.

12. **Weberbauera stenophylla** (Leyb.) Al-Shehbaz, comb. nov.

Draba stenophylla Leyb. Anales Univ. Chile **16:** 679. 1859. *Stenodraba stenophylla* (Leyb.) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 189. 1924. TYPE: Chile, Cord. Santiago, Cerro Colorado, Mapocho Valley, 6000–7000 ft [ca. 1829–2134 m] alt., *Leybold s.n.*[2]

Draba leyboldii Philippi, Linnaea **33:** 10. 1864, non Dalla-Torre & Sarnth. *Stenodraba stenophylla* (Leyb.) O. E. Schulz var. *leyboldii* (Philippi) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 190. 1924. TYPE: Chile, [Región IV, Coquimbo,] Cordillera Doña Rosa, *Volkmann s.n.* (fragment, SGO!).

Draba cauquenensis Philippi, Anales Univ. Chile **81:** 330. 1893. TYPE: Chile, [Región VIII, Maule,] Hacienda de Cauquenes, Cajón del Arriero, *Dessauer s.n.* (lectotype (here designated), SGO!; isolectotypes, B!, M!).

Cespitose perennials. Caudices slender, much branched, the branches terminated in rosettes, covered with petiolar remains of previous years. Stems erect to subdecumbent, (3–)5–13 cm long, glabrous; basal leaves rosulate, petiolate; blades narrowly oblanceolate to rarely spatulate, (1–)1.5–4.5 cm long, (1–)1.5–2(–3) mm wide, subacute to rounded at apex, usually attenuate at base to conspicuous petiole, entire, ciliate with simple trichomes to 1 mm long. Cauline leaves few, subsessile; blades oblong-lanceolate, 4–10(–14) mm long, 1–1.5 mm wide, entire, usually ciliate. Inflorescences ebracteate, corymbose racemes, elongated in fruit. Sepals green to lavender, oblong, 2.5–3 mm long, 1–1.5 mm wide, scarious at margin, glabrous. Petals white, broadly obovate, (3.5–)4–5 mm long, 2–2.5 mm wide, clawed. Filaments white, linear, 2.5–4 mm long; anthers oblong, ca. 0.8 mm long. Fruiting pedicels slender, divaricate-ascending, 5–8(–10) mm long. Fruits oblong to linear, 7–12 mm long, ca. 1.5 mm wide, smooth, glabrous; styles slender, (0.8–)1.5–2 mm long; stigmas entire. Mature seeds not seen.

REPRESENTATIVE SPECIMENS EXAMINED: **Chile.** [REGIÓN VIII, MAULE:] Prov. Curicó, Andes de Curicó, *Vidal s.n.*, 1892 (SGO); El Valle de los Ciegos, near the volcano of Peteroa, *Bridges 1121* (BM, E, GH); Prov. Talca, Cordillera de Talca, *Reiche s.n.* (B); Turrieta, in Cordillera de Talca, *Philippi 1612* (SGO); Prov. Linares, Hacienda de Cauquenes, La Chapa, *Dessauer s.n.*, 1875 (M).

Weberbauera stenophylla is apparently restricted to the three provinces of Región Maule, Chile. I have not seen any recent collections among the holdings of major herbaria. It is not known if the species has become extinct or is very rare and endangered. *Weberbauera stenophylla* is easily distinguished from its closest relatives by characters listed under the preceding species.

[2]According to Stafleu & Cowan (1979), the types and herbarium of Friedrich Leybold, who settled in Chile in 1855, are unknown. However, if the type cannot be located, the detailed original description of the species is accompanied by a well-illustrated plate that should serve as the type.

13. **Weberbauera lagunae** (O. E. Schulz) Al-Shehbaz, comb. et stat. nov.

Stenodraba suffruticosa (Barnéoud) O. E. Schulz var. *lagunae* O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem **10:** 469. 1928. TYPE: Chile, [Región III, Atacama, Prov. Huasco,] Vallenar, Cordillera Laguna Chica, ca. 4000 m alt., Jan. 1924, *Werdermann 262* (holotype, B!; isotypes, BM!, CONC!, GH!, UC!).

Cespitose, scapose perennial. Caudices multibranched, the branches slender, terminated in rosettes, covered with persistent petiolar remains of previous years. Scapes leafless or rarely with small cauline leaf, slender, 2–5(–10) cm long, purplish, glabrous. Basal leaves rosulate, petiolate; blades narrowly oblanceolate to oblong-oblanceolate, 4–10(–15) mm long, (0.5–)1–1.5 mm wide, rounded at apex, somewhat attenuate at base, entire, flat, glabrous beneath, densely ciliate and hispid above with unbranched trichomes to 1 mm long, midrib prominent; petioles persistent, thick, subterete, 1–5 mm long. Inflorescences ebracteate, few-flowered, corymbose racemes, elongated considerably in fruit. Sepals oblong, 1.5–2 mm long, 0.8–1 mm wide, nonsaccate, pubescent with straight trichomes. Petals yellowish white, with purplish area on back, oblong, 1.5–1.7 mm long, 0.4–0.8 mm wide, undifferentiated into blades and claws. Filaments 1.2–1.5 mm long; anthers oblong, 0.5–0.6 mm long. Fruiting pedicels divaricate to occasionally divaricate-ascending, slender, 4–8(–12) mm long, glabrous. Fruits linear, terete, torulose, 7–11 mm long, 0.9–1.2 mm wide, tapering at both ends, glabrous; septa hyaline; styles 0.3–0.4 mm long; stigmas entire. Seeds uniseriately arranged in each locule, oblong, 1.2–1.3 mm long, ca. 0.7 mm wide, brown; funicles thickened at placental end.

Growing on dry rocky slopes and gravelly, sod-covered banks at altitudes of 3800–4000 m.

REPRESENTATIVE SPECIMENS EXAMINED. **Chile.** [REGIÓN III, ATACAMA:] Prov. Huasco, vicinity of Laguna Chica, *Johnston 5950* (GH); vicinity of Laguna Valeriano, *Johnston 6056* (CONC, GH, US).

Although *Weberbauera lagunae* was originally described by Schulz (1928) as a variety of *Stenodraba suffruticosa* (now *W. suffruticosa*), it is so different in leaves, flowers, and fruits from both this and the closely related *W. imbricatifolia* that it should be recognized as a distinct species. *Weberbauera lagunae* has narrowly oblong, nonclawed petals less than 2 mm long and styles 0.3–0.4 mm long in fruit. In contrast, both *W. imbricatifolia* and *W. suffruticosa* have clawed, broadly spatulate petals 3.5–5.5 mm long and styles 1–3 mm long in fruit. Furthermore, *W. lagunae* differs from *W. imbricatifolia* in having the lower leaf surface glabrous instead of pubescent, and from *W. suffruticosa* in having the leaves flat and oblanceolate instead of semiterete and linear.

Weberbauera lagunae differs from the related *W. colchaguensis* in having lax, racemose infructescences, slender, divaricate fruiting pedicels 4–8(–12) mm long, torulose fruits, and entire basal leaves to 1.5 mm wide. *Weberbauera colchaguensis* has dense, subumbellate infructescences, stout, subappressed fruiting pedicels 1.5–4.5(–6) mm long, smooth fruits, and usually dentate basal leaves 2–4.5(–6) mm wide.

14. **Weberbauera suffruticosa** (Barnéoud) Al-Shehbaz, comb. nov.

Draba suffruticosa Barnéoud *in* C. Gay, Fl. Chile **1:** 157. 1846. *Sisymbrium suffruticosum* (Barnéoud) Fourn. Rech. Anat. Tax. Fam. Crucif. (Thesis, Paris), 132. 1865. *Hesperis suffruticosa* (Barnéoud) Kuntze, Revis. Gen. Pl. **2:** 935. 1891. *Draba imbricatifolia* Bernéoud var. *suffruticosa* (Barnéoud) Reiche, Fl. Chile **1:** 116. 1896. *Stenodraba suffruticosa* (Barnéoud) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 190. 1924. TYPE: Chile, [Región IV, Coquimbo,] Cordillera Ovalle, 12,000 ft [ca. 3658 m] alt., *Gay s.n.* (holotype, P; isotype, B! (photos, GH!, MO!)).

Cespitose, scapose perennial. Caudices branched, the branches slender, terminated in rosettes, covered with petiolar bases of previous years. Scapes leafless or rarely with 1 or 2 leaves, 3–5 cm long, glabrous. Basal leaves rosulate, petiolate; blades linear, thick, usually semiterete, (3–)4–8 mm long, 0.5–0.8 mm wide, the margin somewhat incurved, entire, ciliate, the lower surface glabrous, the upper surface usually densely hispid with simple trichomes to 1 mm long; midribs and petioles persistent. Inflorescences ebracteate, few-flowered racemes, elongated and lax in fruit. Sepals erect, oblong, 3.5–4 mm long, nonsaccate, scarious at margin, usually pubescent with straight, simple trichomes. Petals broadly spatulate, 4.5–5.5 mm long, ca. 1.5 mm wide, rounded at apex, attenuate to distinct, clawlike base. Filaments 3–3.5 mm long; anthers oblong, ca. 1 mm long. Fruiting pedicels divaricate, slender, (6–)8–12 mm long, glabrous. Fruits linear, subterete, somewhat torulose, 11–16 mm long, glabrous; septa hyaline; styles slender, (1.5–)2–3.1 mm long; stigmas entire. Seeds uniseriately arranged in each locule, oblong, ca. 1.5 mm long, 0.8 mm wide, brown; funicles somewhat stout at placental end.

REPRESENTATIVE SPECIMENS EXAMINED. **Chile.** [REGIÓN IV, COQUIMBO:] Prov. Limarí, Sotaquí, *Gay 1029* (SGO); Cordillera de Doña Rosa, *Volckmann s.n.*, 1860/1861 (SGO); Quebrada Larga, *Jiles 3408* (CONC).

Weberbauera suffruticosa, which is very rare and apparently known only from few collections, is easily distinguished from all other species of the genus by its semiterete, thick, linear basal leaves 0.5–0.8 mm wide. It also differs from its closest relative, *W. imbricatifolia,* in having a glabrous lower leaf surface. Both species have large flowers and slender styles to 3 mm long.

15. **Weberbauera imbricatifolia** (Barnéoud) Al-Shehbaz, comb. nov.

Draba imbricatifolia Barnéoud *in* C. Gay, Fl. Chile **1:** 158. 1846. *Braya imbricatifolia* (Barnéoud) A. Gray, U. S. Expl. Exped. Phan. **15**(1): 58. 1854. *Sisymbrium imbricatifolium* (Barnéoud) Wedd. Chloris Andina **2:** *t. 58B.* 1857. *Hesperis imbricatifolia* (Barnéoud) Kuntze, Revis. Gen. Pl. **2:** 934. 1891. *Stenodraba imbricatifolia* (Barnéoud) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 190. 1924. TYPE: Chile, [Región IV, Coquimbo,] Cordillera de Coquimbo, 12,000 ft [ca. 3658 m] alt., *Gay s.n.* (holotype, P; isotype, B! (photo, MO!); probable isotypes, G!, GH!).

Stenodraba imbricatifolia (Barnéoud) O. E. Schulz var. *glabrata* O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 190. 1924. TYPE: Chile, *Leybold 2974* (holotype, B!).

Cespitose, scapose perennial. Caudices woody, much branched, the branches terminated in rosettes, covered with persistent petiolar bases of previous years.

Scapes leafless or rarely with 1 or 2 cauline leaves, (0.6–)1–4(–6) cm long, glabrous. Basal leaves petiolate, flat; blades oblong to rarely oblanceolate, 2–7(–15) mm long, 0.5–1.5(–2) mm wide, rounded at apex, entire, ciliate, densely hispid above with simple trichomes to 1 mm long, pubescent below with much shorter, branched or rarely simple trichomes, very rarely glabrescent; petioles persistent, thick, 0.5–3(–5) mm long. Inflorescences few-flowered, ebracteate, corymbose racemes, elongated in fruit. Sepals erect, oblong, (2–)2.5–3.5 mm long, 1–1.5 mm wide, nonsaccate, scarious at margin, pubescent. Petals white, broadly spatulate, 3.5–5 mm long, 1.5–2 mm wide, rounded at apex, tapered to short claw. Filaments erect, 3–4 mm long; anthers oblong, ca. 1 mm long. Fruiting pedicels divaricate to ascending, slender, 3–7(–10) mm long, glabrous. Fruits linear, terete, somewhat torulose, (7–)9–14(–16) mm long, 1.2–1.5 mm wide, glabrous; septa hyaline; styles slender, 1–2(–3) mm long; stigmas entire. Seeds uniseriately arranged in each locule, oblong, ca. 1.2 mm long, 0.8 mm wide, brown.

REPRESENTATIVE SPECIMENS EXAMINED. **Chile.** [Región IV, COQUIMBO:] Prov. Choapa, Cordillera de Illapel, Vega Negra, *Volckmann s.n.*, 1860/1861 (SGO); La Polcura, *Philippi 2279* (SGO). [REGIÓN V, ACONCAGUA:] Prov. Petorca, 5 km S of Junta de Piuquenes, Río Sobrante, *Morrison 17290* (DS, UC). [REGIÓN VI, METROPOLITANA DE SANTIAGO:] Prov. Santiago, Andes of San José, *Gay 1028* (SGO).

Weberbauera imbricatifolia is highly variable in the size and pubescence of the basal leaves. Schulz (1924) used the leafless scapes and short (2–4 mm) basal leaves of this species to distinguish it from *W. suffruticosa* (both as *Stenodraba*). *Weberbauera suffruticosa* was said to have few cauline leaves and longer (6–8 mm) basal ones. The presence of cauline leaves is uncommon in both species, and different rosettes of the same plant might produce leafless stems, as well as stems with one or two leaves. Furthermore, the length of basal leaves is unreliable for the separation of these species (see descriptions). The shape, pubescence, and cross section of basal leaves provide the most reliable distinguishing characters: the leaves of *W. imbricatifolia* are flat, oblong to rarely oblanceolate, and almost always pubescent beneath with simple or furcate trichomes shorter than those of the upper surface; in contrast, those of *W. suffruticosa* are thick, semiterete, and linear, with a glabrous lower surface.

16. **Weberbauera parvifolia** (Philippi) Al-Shehbaz, comb. nov.

Sisymbrium parvifolium Philippi, Linnaea **28**: 667. 1856. *Stenodraba parvifolia* (Philippi) O. E. Schulz, Pflanzenr. IV. **105**(Heft 86): 187. 1924. TYPE: Chile, [Región VIII, Maule,] Cordillera de Linares, *Germain s.n.*, 1856 (holotype, SGO *63217*!).

Cespitose perennials. Caudices slender, much branched, the branches terminated in rosettes. Stems erect or subdecumbent, simple or branched at base and/or above, 6–15(–25) cm long, glabrous or sparsely pubescent with furcate and/or dendritic trichomes. Basal leaves rosulate, short petiolate to subsessile; blades narrowly oblanceolate to rarely subovate, 5–20(–35) mm long, 1–2.5(–3.5) mm wide, obtuse to subacute, cuneate to attenuate at base, entire or rarely dentate, ciliate with simple trichomes, often with branched trichomes on surface, flat. Cauline leaves few, smaller and narrower than basal ones. Inflores-

cences ebracteate, corymbose racemes, elongated in fruit. Sepals caducous, oblong, 1.5–2.6 mm long, 0.7–1 mm wide, glabrous or with dendritic trichomes. Petals white, oblanceolate, (1.8–)2.5–3.5 mm long, to ca. 1 mm wide. Filaments white, 1.7–2.8 mm long; anthers oblong, 0.6–0.8 mm long. Fruiting pedicels divaricate, straight, 4–10(–16) mm long, usually glabrous. Fruits linear, flattened, not torulose, 8–18(–24) mm long, 0.8–1.2(–1.5) mm wide; valves glabrous, with conspicuous midvein; styles 0.1–0.4(–0.7) mm long; stigmas entire. Seeds uniseriately arranged, oblong-ovate, 1.2–1.6 mm long, 0.7–0.9 mm wide, brown; cotyledons incumbent; funicles somewhat thickened at proximal end.

Representative specimens examined. **Argentina.** Prov. Neuquén: Depto. Lacar, Chapelco, *Schajovskoy 61* (BAA); Depto. Chos Malal, cajón del ao. del Cruce, *Boelcke, Correa, Bacigalupo, et al. 11279* (BAA); Depto. Minas, confluence of rivers Pichi-Neuquén and Neuquén, *Boelcke et al. 13763* (BAA); upper valley of ao. Atreuco, *Boelcke, Correa, Bacigalupo, et al. 11512* (BAA), *11533* (BAA, SI); Cordillera del Viento, cruzada de Tricao Malal al Cajón de Butaló, *Boelcke, Correa, Bacigalupo, et al. 11565* (BAA, SI); Cajón de los Chenques, *Boelcke et al. 13847* (BAA); N of Varvarco Campos, *Boelcke et al. 14144* (BAA); Depto. Picunches, Pino Hachado, *Burkart 9738* (SI); Lago Aluminé, *Kalela 1608* (H). **Chile.** [Región VII, Del Libertador General Bernardo O'Higgins:] Prov. Colchaqua, San Fernando, Termas El Falco, *Montero 6043* (SI). [Región VIII, Maule:] Cordillera de Maule, *Germain s.n.*, 1856–1857 (G); Prov. Talca, Cordillera de Talca, El Picazo, *Barros 2752* (SI).

Weberbauera parvifolia is somewhat anomalous in the genus in having sometimes erect stems that are branched above. No other species of *Weberbauera* has this feature. However, *W. parvifolia* is related to other species of the genus that Schulz (1924) placed in *Stenodraba*.

ACKNOWLEDGMENTS

I am most thankful to Reed C. Rollins and Neil A. Harriman for their critical reviews of the manuscript, and to Donald H. Pfister for obtaining funds from the Harvard University Herbaria that supported the SEM portion of the research. I am grateful to Elizabeth A. Shaw and Peter F. Stevens for correcting the Latin diagnoses, Gustavo A. Romero for helping with Spanish, Michael A. Canoso for obtaining the loans, Barbara Nimblett for typing the manuscript, Trisha Rice for the SEM work, my wife, Mona, for her continuous support, and Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice. I am indebted to Stephan G. Beck, Clodomiro Marticorena, Barbara Ruthsatz, David N. Smith, and James C. Solomon for sending plant material. I thank the directors and curators of the herbaria (abbreviations follow Holmgren *et al.*, 1981), who kindly loaned the specimens on which this study is based.

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PRELIMINARY TAXONOMIC CONSIDERATION OF THE PORANEAE (CONVOLVULACEAE)

GEORGE W. STAPLES[1]

The tribe Poraneae (Convolvulaceae) has been taxonomically evaluated, and some realignment of genera is necessary. *Metaporana* N. E. Br. is here reassigned to the tribe Cresseae. A new combination is made for a species endemic to Socotra; its diagnostic features are discussed. *Dactylostigma* D. Austin is reduced to synonymy with *Hildebrandtia* Vatke ex A. Braun of the tribe Hildebrandtieae. A new name is provided for the first Madagascan species of *Hildebrandtia*.

Eight genera had been assigned to the Poraneae Hallier f. (Convolvulaceae) (see TABLE) when I began an evaluation of the tribe in 1983. Of these, some were questionably placed because they appeared to lack the characters used by Hallier (1893) to establish the tribe—namely, an accrescent, winglike fruiting calyx enclosing a one-seeded, indehiscent fruit with a papery pericarp (utricle).

A comprehensive examination of all genera assigned to the tribe Poraneae is nearing completion. The present paper will provide an overview of the tribe and make necessary taxonomic combinations for two genera being removed from the Poraneae. The next paper will present a taxonomic revision of the genus *Porana* Burman f., which formed the bulk of my doctoral dissertation (Staples, 1987). The final one will recharacterize the tribe Poraneae and delimit the character states for the genera assigned to it; it will also include revisions for the genera *Cordisepalum* Verdc., *Cardiochlamys* Oliver, *Rapona* Baillon, and *Dipteropeltis* Hallier f. Within the genus *Calycobolus* the African taxa have been studied by Lejoly and Lisowski (1985) and the Neotropical taxa by Austin and Staples (in prep.). In addition, a comprehensive palynotaxonomic study of this genus and its close relative *Dipteropeltis* is nearing completion (D. Vernier, pers. comm.) and will perhaps further illuminate the relationships of these genera. These works account for most of the genera that had been assigned to the Poraneae prior to 1983, when I began this study.

Two genera, *Metaporana* N. E. Br. and *Dactylostigma* D. Austin, remain to be discussed. Based on morphological, palynological, and trichome characters, they are incorrectly referred to the Poraneae. They are here reassigned to other tribes, necessitating one new name and one new combination.

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Journal of the Arnold Arboretum **71**: 251–258. April, 1990.

A conspectus of the tribe Poraneae Hallier f.* ca. 1983.

GENUS	DATE OF FIRST PUBLICATION	NUMBER OF TAXA	PROVENANCE
Porana Burman f.	1768	ca. 25	Asia and Australia
Calycobolus Willd.	1819	ca. 20	W Africa and tropical America
Cardiochlamys Oliver	1883	2	Madagascar
Rapona Baillon	1891	1	Madagascar
Dipteropeltis Hallier f.	1899	2	W Africa
Metaporana N. E. Br.	1914	7	E Africa and Madagascar
Cordisepalum Verdc.	1971	1	SE Asia
Dactylostigma D. Austin	1973	1	Madagascar

*Adapted from Austin (1973).

METAPORANA

Nicholas Brown (1914) established *Metaporana* for two East African taxa. Since that time, the genus has variously been maintained as distinct (Myint & Ward, 1968; Verdcourt, 1969) or placed in synonymy with *Bonamia* Thouars (Meeuse, 1957; Verdcourt, 1963). Myint & Ward (1968), in their revision of *Bonamia,* concluded that *Metaporana* was distinct from *Bonamia.* Reexamination of *Metaporana* in terms of the characters used to define the Poraneae, however, revealed that its persistent but nonaccrescent calyx and tardily dehiscent capsule exclude it from that tribe. Overall morphology, trichomes, and pollen characters of *Metaporana* indicate that it is better placed in the tribe Cresseae Bentham & Hooker, a reassignment I here effect. The Cresseae, in need of careful systematic scrutiny, are at best loosely delimited at present by their branched style or two free styles, dehiscent capsules, nonaccrescent calyces, and predominantly nonspinose, three-colpate pollen grains.

Verdcourt (1969) accepted *Metaporana* as a valid genus and lectotypified it with *M. densiflora* (Hallier f.) N. E. Br., simultaneously recognizing the first Madagascan species of the genus, *M. parvifolia* (K. Afzel.) Verdc. He later (1974) identified three varieties of the latter species, *M. parvifolia* var. *obovata,* var. *obtusa,* and var. *pilosa,* and described two additional species endemic to Madagascar, *M. conica* and *M. sericosepala.* Since his 1974 paper describes, illustrates, and lists specimens examined for the Madagascan taxa, such information is not repeated here. A description and illustration for *M. densiflora* are available in Verdcourt (1963, under *Bonamia poranoides*). I do include a list of representative specimens examined for this widely distributed African plant.

This brings to four the number of species in *Metaporana,* one in East Africa and three from Madagascar. To these I can add another, which was described as a species of *Porana. Porana obtusa* Balfour f. is endemic to the island of Socotra. Only one additional collection has come to light since Balfour's gathering of the type material. The slightly accrescent fruiting calyx and tardily

dehiscent, two-seeded capsule exclude the species from *Porana* and indicate a placement in *Metaporana*.

Metaporana obtusa (Balf. f.) Staples, comb. nov.

Porana obtusa Balf. f. Proc. Roy. Soc. Edinburgh **12:** 83. 1883; Trans. Roy. Soc. Edinburgh **31:** 192. *t. 57.* 1888. TYPE: Socotra, "inter scopulos ad extremitatem campi Kadhab scandens," Feb.–March 1880, *Balfour, Cockburn, & Scott 355* (holotype, K!; isotypes, BM!, E!, LE!; fragment, GOET!).

Little can be added to the 1888 description published by Balfour, which in conjunction with his plate, adequately characterizes the species. *Metaporana obtusa* is an erect shrub 3–10 m tall, with leathery, dull-colored, oblong leaves having an obtuse to emarginate apex and 12 to 14 pairs of secondary veins. The corolla lobes are marked with dark, elliptic (? glandular) dots, and the capsule has a glossy, resinous-looking surface, much like that of *M. sericosepala* Verdc. Overall, *M. obtusa* has the largest fruiting calyx of any species in the genus due to the slightly accrescent nature of the sepals.

DISTRIBUTION. Endemic to the island of Socotra in the Indian Ocean.

ADDITIONAL SPECIMEN EXAMINED. **Socotra Island**: Ras Kattomahan, *G. Popov So/136* (BM).

Metaporana densiflora (Hallier f.) N. E. Br. Bull. Misc. Inform. **1914:** 168. 1914.

Porana densiflora Hallier f. Bot. Jahrb. Syst. **18:** 93. 1894; *in* Engler, Abh. Preuss. Akad. Wiss. 26, 34. 1894. TYPE: East Africa, 1885–1886, *Fischer 284* (holotype, B, destroyed; fragment, GOET!).

Bonamia poranoides Hallier f. Bull. Herb. Boissier **5:** 1007. 1897, nom. nov., non *B. densiflora* (Baker) Hallier f. (1894).

DISTRIBUTION. Widespread in equatorial Africa, from northeastern Zaïre eastward through Uganda, Tanzania, and Kenya to the Indian Ocean.

REPRESENTATIVE SPECIMENS EXAMINED. **Kenya.** COAST PROV. Kilifi distr.: Kilifi, *G. M. Jeffrey K307* (K), *Graham 1923* (K); Mnarani, *Lavranos 11899* (M); Mtawapa, *Williams Sangrai 840* (K); Sabaki, 4 mi N of Malindi, *R. Polhill & Paulo 734* (K, P). Kwale distr.: behind Diani Beach, *J. B. Gillett 18645* (K, P); Diani Forest, *J. B. Gillett & Kibuma 19879* (K). Mombasa distr.: Bamburi–Shimo la Tewa, *Bally & A. R. Smith 14380* (K); Mombasa, *Sacleux 2208(#1)* (P), *2208(#2)* (P). Distr. not indicated: Jardini Forest, *Foden & A. Evans 70/409* (K); Kibarani, *G. M. Jeffrey K53* (K); N of Mombasa to Lamu and Witu, *A. Whyte s.n.,* 1902 (BM); Mombasa to Takaungu, *A. Whyte s.n.,* 1902 (K); S of Mombasa, *H. M. Gardner 1413* (K); Mwachi, 3 mi S of Mazeras, *R. B. Drummond & J. H. Hemsley 4245* (K); Rabai Hills, Mombasa, Mlima von Riali, Rabai, *W. E. Taylor s.n.,* Sept. 1885 (BM); Shanzu, *E. Polhill 408* (K, P); Takaungu, *Thomas s.n.,* Feb. 1867 (WU). SOUTHERN PROV., distr. not indicated, Kitui, Endau forest, *J. Mbonze 31* (K). **Tanzania.** EASTERN PROV. Dar es Salaam, Wazo Hill, *Batty 37* (P), *1071* (P). Kisarawe distr.: Kazimzumbwe, *Proctor 6* (K); Nyaburu, *T. H. Fundi s.n.,* 18 May 1954 (K); Pugu Hills, forest reserve, *O. J. Hansen 431* (C), *J. H. Vaughan 2342* (BM). TANGA PROV. Pangani distr.: Bushiri Est., *Faulkner 590* (BM, K, P, S); Mecca Parish, Mseko section, Mwera chiefdom, *Tanner 2943* (UC); Pangani, *Stuhlman 594* (HBG). Distr. not indicated: Kigombe, *Geilinger 897* (K); Kirindani, *H. Faulkner 3612* (BR); 4 mi SE of Ngomeni, *R. B. Drummond & J. H.*

Hemsley 3608 (K); Usambara Mtns., Bŭiti, *Holst 2379* (K, M); Usambara Mtns., Duga, *Holst 3205* (BM, G, HAM, K, LE, M, P, S, US, W); Usambara Mtns., Maramba, Mwele, *Peter 51724* (B, GOET); Usambara Mtns., bei Masbura, *Peter 51624* (GOET); Usambara Mtns., Mkumbora, *Doughty 2* (K). Prov. not indicated, Krogwe distr., Magewga Est., *Faulkner 1335* (K). **Uganda.** EASTERN PROV. Busoga distr.: Butembe-Bunya Co., 12 mi N of Jinja, Kagoma Forest Reserve, *G. H. S. Wood 321* (K); Wandago Mutalla, ca. mi 10 on new Iganga road, *G. H. S. Wood 18* (K); without further locality, *E. Brown 369* (K). Distr. not indicated, Aga Swamp, Teso country, *P. Chandler 987* (K). WESTERN PROV. Toro distr., Ruwenzori, *G. Taylor 2662* (BM). Distr. not indicated: Butiaba, plain on E shore of Lake Albert, *Bagshawe 843* (BM); 58 mi from Fort Portal, SW of Mukokya, *Lock 463* (K); Kikonongo, Ruenzori, *Maitland 1037* (K). Prov. and distr. not indicated: Bwamba, *R. Fyffe 19* (K); Commo, shores of Nyanza Salt Lake, *Scott-Elliot 7972* (BM, K); Plucot (Usoga), *R. Dümmer 2790* (BM); Waryanga-Jinja, *P. Chandler 2066* (K, P). **Zaïre.** PROV. KIVU. Beni territory: Beni, *Lebrun 4599* (K, US); Bwambali, Parc Natl. Albert, *De Witte 13942* (K). Territory not indicated: Bitshumbi [Vitshumbi], Bosquet, *Lebrun 9269* (BR, K, MO, P); Bitschumbi, Kikongomoko, *De Witte 1035* (BR, K); Kabare, *Bequaert 5424* (BR); Kotonda [Katanda], *Lebrun 7705* (K, P); NO Kongo, Semliki-Ebena, *Mildbraed 2129* (HBG). PROV. ORIENTALE, Ituri, versant Ouest, massif du Ruwenzori, *H. Humbert 8809* (P). Prov. not indicated: Ruindi, *Lebrun 8029* (K, P); près du camp de la rivière Ruindi, *De Witte 2083* (K).

A comment on the typification of this species is warranted. The holotype for *Porana densiflora* was destroyed with the Berlin herbarium, and no isotype has come to light that might serve as lectotype. This situation prompted Verdcourt (1963) to designate *Holst 3205* (K) as a neotype for the name. In the material loaned for the tribal revision, I found a fragment of the original Fischer collection conserved at Goettingen. Perhaps Hallier removed a bit of the holotype from Berlin for his studies at Goettingen, where he worked for some time. In any case, the application of the name is without question because *Fischer 284* is the same species as *Holst 3205*. Although the latter collection now has no nomenclatural standing, it is useful for comparative purposes because it has been authenticated by comparison with the only fragment of the holotype known to exist. The Holst collection has been widely distributed and is more readily available to botanists than the original Fischer collection.

DACTYLOSTIGMA

Based on a single poorly preserved specimen from Madagascar, Austin (1973) described the genus *Dactylostigma*, typified by *D. linearifolia*. The generic name refers to the highly divided stigmas, lobed like the fingers of a hand, which Austin believed were unique in the Convolvulaceae. The holotype specimen is depauperate, and although stigmas are visible, the other structures inside the flowers are largely obscured by fungal hyphae. The spent flowers are enclosed in large, papery calyces, with the two outer sepals much accrescent, the third sepal less so, and the fourth and fifth ones only slightly increased in size. The fruits, which are immature on the holotype specimen, are formed from a unilocular ovary containing four ovules, only one of which develops into a seed. These features suggest a relationship to the Poraneae, to which tribe Austin referred the new genus.

During a visit to the Paris herbarium in 1984, I was able to examine the

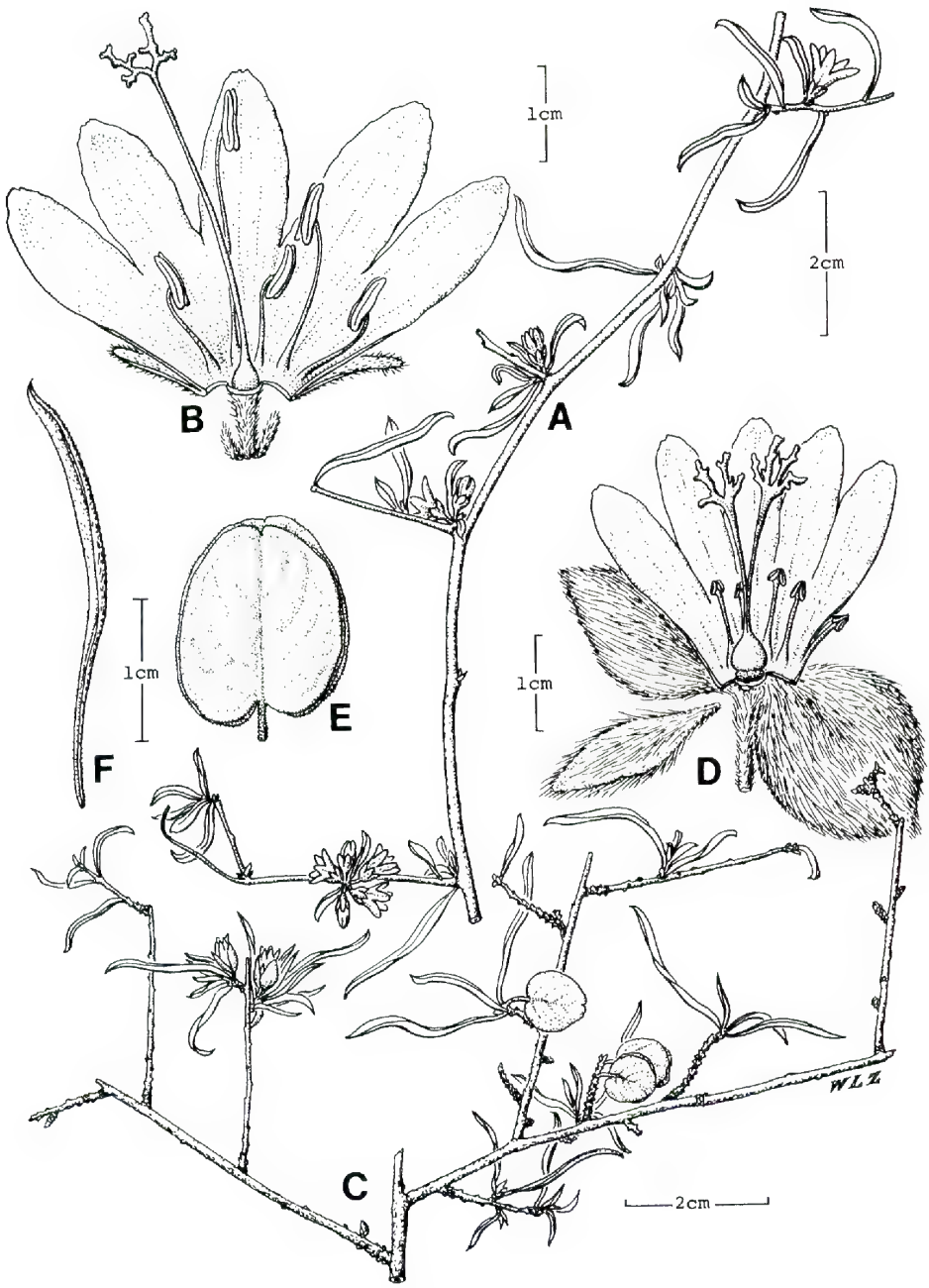
very rich Madagascan collections conserved there. Having studied additional, more complete material of *Dactylostigma,* I can now amplify Austin's description of the plant. The flowers are functionally unisexual, with staminate and pistillate flowers borne on separate plants. I was able to compare these specimens with complete material of *Hildebrandtia* Vatke and *Cladostigma* Radlk., two African genera known to be dioecious (Hallier, 1898). The stigmas of *Dactylostigma* proved to be identical to those of *Hildebrandtia,* although the Madagascan plants are clearly a different species of that genus than any of those known from Africa (Verdcourt, 1961, 1981). Austin (pers. comm.) saw no comparative material of *Hildebrandtia* when he described *Dactylostigma* and thus did not realize that his novelty was in fact the first species of *Hildebrandtia* from Madagascar.

I here reduce *Dactylostigma* to synonymy with *Hildebrandtia,* which has been placed in the tribe Hildebrandtieae Peter (Melchior, 1964; Roberty, 1964; Willis, 1973) due to the dioecious habit, a feature unique in the Convolvulaceae. The epithet *linearifolia* is preoccupied in *Hildebrandtia,* so a new name is required. I take the opportunity to name the first Madagascan species of the genus in honor of Daniel F. Austin, who has contributed greatly to an improved understanding of the complex relationships in the Convolvulaceae.

Hildebrandtia austinii Staples, nom. nov. FIGURE.

Dactylostigma linearifolia D. Austin, Phytologia **25:** 426. 1973, non *Hildebrandtia linearifolia* Verdc. (1981). TYPE: Madagascar, delta de la Linta, côte SW, 24–28 Aug. 1928, *Humbert & Swingle 5368* [♀] (holotype, MO!; isotype, P!).

Slender, scandent shrub, 0.5–2 m long, rufous-golden-sericeous on young parts, glabrate with age. Stems slender, virgate, nodes laxly spaced, main axes grayish and smooth, short shoots warty due to leaf scars, tips golden-sericeous. Leave clustered in fascicles at nodes or on lateral short shoots, subsessile, folded lengthwise in dried state; blade linear to oblong or narrowly obovate, 4–20 × ≤1 mm, base cuneate, apex acute or obtuse and apiculate, margin entire, both surfaces shining-golden-sericeous. Flowers borne among leaves, 1 to few per node, sessile or on pedicels ≤2 mm long (in fruit lengthening to 5–6 mm), 5-merous. Staminate flowers with sepals ±equal, elliptic-oblong, 2–3 × ≤1 mm, sericeous; corolla campanulate, 5-lobed, 5–6 mm long, white, sericeous outside, glabrous within; stamens barely exserted, unequal, 3–5 mm long, the filaments fused below to corolla tube and sparsely glandulose, free, filamentous, and glabrous above, the anthers dorsifixed, ellipsoid, introrse, whitish; pollen spheroidal, 15–18 μm in diameter, 3-colpate, surface finely granulate; pistillode with rudimentary ovary, the style 1, simple, the stigma deeply palmately dissected. Pistillate flowers with sepals unequal (the outer 2 larger, broad-ovate, ca. 5 × 3 mm, base oblique, apex acute; median one ovate, oblique, inner 2 oblong-lanceolate), chartaceous, sericeous on both surfaces; corolla campanulate, 5-lobed, ca. 5 mm long, white, the lobes sericeous outside, glabrous within; staminodes unequal, ≤2 mm, nonpolliniferous; disc pedestallike; ovary ovoid, 4-lobed, ca. 1 mm tall, glabrous; ovules 4; styles 2, free, filiform, glabrous; stigmas deeply palmately lobed. Capsule (immature) narrowly ovoid,



Hildebrandtia austinii: A, staminate plant, habit; B, staminate flower, corolla open; C, pistillate plant, habit; D, pistillate flower, corolla open; E, fruiting calyx; F, leaf. (A, B after *Rakotomama & Surveillant 3929*; C, D after *Humbert & Perrier de la Bâthie 2423*; E, F after *Humbert & Swingle 5368*.) Drawing by Wang Le-zhong.

1-seeded, tan to pale brown, glabrous, surmounted by persistent corolla and enclosed in accrescent calyx, the outer 2 sepals ovate, 13–20 × 10–14 mm, the middle one ovate-elliptic, oblique, 13 × 9 mm, the inner 2 oblong, 8–9 × ca. 2 mm, all sepals chartaceous, villous on both surfaces. Seeds ovoid, carinate, ca. 2 mm long, dark brown, smooth, glabrous, with basal hilum.

DISTRIBUTION AND ECOLOGY. Endemic to Madagascar (known only from southwest coast in vicinity of Tuléar); sandy and lateritic soils 2–10 m alt. Flowering March to September, fruiting August and September.

VERNACULAR NAMES. Vongo, rakiorakitz.

SPECIMENS EXAMINED. **Madagascar.** Betioky distr.: Soalary canton, Reserve Naturelle X, *Ravelonanabary 5017* [♀] (P), *Rakotomama & Surveillant 3929* [♂] (P). Distr. not indicated: env. du Tuléar, delta du Fiherenana, *Humbert & Perrier de la Bâthie 2403* [♂] (P), *2423* [♀] (P); km 4 de Tuléar, *Service Forestier SF 16981* [♂] (P); env. de Tuléar, *Perrier de la Bâthie 12834* [♂] (P).

The linear-oblong leaves of *Hildebrandtia austinii* set it apart from most other species of the genus. Only *H. linearifolia,* from Somalia, could be confused with it on the basis of leaf shape. The two species can be readily distinguished, however, by the differences in their habit and the nature of their fruiting sepals. *Hildebrandtia austinii* has slender, scandent stems with laxly arranged fascicles of leaves; the two outer fruiting sepals are ovate and are villous on both sides. In contrast, *H. linearifolia* is a shrub with stout stems and spinescent branches, with the fascicles of leaves crowded along them; the two outer fruiting sepals are orbicular and are appressed-pubescent on the abaxial side only.

The flowers of *Hildebrandtia austinii* provide another character that may prove taxonomically useful, once the character states are known in other species of *Hildebrandtia.* The pistillate flowers have a gynoecium with two free styles, each terminating in a digitate stigma, whereas the staminate ones have a pistillode with a single style terminating in a pair of digitate stigmas. In other species for which this character is known, such as *H. africana* Vatke, flowers of both sexes have the style divided to the base (Miller & Morris, 1988).

One collection, *Ravelonanabary 5017,* has spherical hairy bodies in the axillary position usually occupied by flowers or fruits. These structures may be teratological byproducts (galls?) caused by infection of the reproductive organs with a pest or pathogen.

ACKNOWLEDGMENTS

This research was conducted while I was a doctoral student at Harvard University in the Department of Organismic and Evolutionary Biology, where I utilized the collections and libraries of the combined Harvard University Herbaria. Travel funds, which permitted me to visit British and European herbaria, were made available through the Atkins Fund and the Anderson Fund, both of Harvard University. This proved to be an exceptionally rewarding opportunity. I am indebted to Dr. Jean Leroy, Muséum National d'Histoire Naturelle, Paris, who authorized the loan of critical material on which this paper is based. Two reviewers, K. R. Robertson and B. Verdcourt,

offered their suggestions for the improvement of the manuscript. The illustration of *Hildebrandtia austinii* was prepared by Mr. Wang Le-zhong, whose skill as a botanical illustrator I salute. The larger research program, of which this paper represents only the first part, was supported by the National Science Foundation, Dissertation Improvement Grant BSR 85 00832. I deeply appreciate the financial and material support provided by these institutions and individuals.

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NOTES ON A NOVEL ABAXIAL LEAF EPIDERMIS IN ECUADORIAN BEGONIA PARVIFLORA

W. Scott Hoover[1, 2]

Scanning-electron-microscope observations and stomatal-density counts indicate that two populations of Ecuadorian *Begonia parviflora* have very different surface epidermal characteristics. Compared to a population near Baños, Ecuador, a population near Tena has novel epidermal characteristics, including a mean stomatal density of 634.7 ± 26.2 stomata per mm^2, guard cells raised on cellular protrusions above the surrounding epidermal cells, and epidermal cells appearing indistinguishable from subsidiary cells. High stomatal density may be of adaptive significance to higher light, or exposure, intensity, although the possibility exists that raised guard cells and comparatively small epidermal cells are an architectural consequence of high stomatal density originating during early leaf development.

The genus *Begonia* L. is recognized for its unusual leaf anatomy, with many species having a multilayered epidermis (Fellerer, 1892; Solereder, 1908; Haberlandt, 1909; Metcalfe & Chalk, 1950; Foster & Gifford, 1959; Esau, 1965). Numerous species of *Begonia* have stomatal clusters, a characteristic limited to species in only a few unrelated angiosperm families (Fellerer, 1892; Metcalfe & Chalk, 1950; Neubauer, 1967; Boghdan & Barkley, 1972; Skog, 1976; Hoover, 1986). By contrast, other *Begonia* species have singly occurring stomata as well, which is the pattern exhibited by *B. parviflora* Poep. & Endl. This species is distributed at lower elevations on both the Amazonian and Pacific slopes of the Andes from Colombia to Peru. It is distinct from most species in the genus because it is a small tree (Smith & Schubert, 1941, 1946; Smith & Wasshausen, 1979). One of the most common Andean species of *Begonia, B. parviflora* is observed frequently as individuals or small populations and occasionally in colonies comprising many individuals.

In this study two populations of *Begonia parviflora* are compared for characters of the abaxial leaf epidermis. Although the populations grow in the same region, they differ considerably in density of stomata, length of stomatal pores, structural anatomy of guard cells, and size of epidermal cells.

METHODS AND MATERIALS

On February 3, 1984, two colonies of *Begonia parviflora* were sampled on the Amazonian slope of the Andes in Ecuador. The species was frequently

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Journal of the Arnold Arboretum **71**: 259–264. April, 1990.

observed throughout this region, with the colonies sampled being among the largest observed. The Baños colony was growing in moderate shade with successional vegetation 12 km east of Baños, Tungurahua Province (lat. 01°14′N, long. 78°22′W), at 1548 m altitude. The Tena population was observed at an exposed site 59 km north of Puyo, Napo Province (lat. 01°14′N, long. 77°53′W), at 906 m altitude. One leaf from each of ten healthy individual plants was collected at each population site, and clear fingernail polish was immediately applied to the lower leaf surfaces, allowed to dry thoroughly, then peeled off with forceps (Sampson, 1961).

In the laboratory the epidermal replicas were projected on a screen using an Edmund Scientific microprojector. Stomatal counts and measurements were made on a single mm^2 area from each peel. Lengths of five stomatal pores were measured on each peel and the mean determined. One clear epidermal replica was chosen from each population for permanent fixation for scanning-electron-microscope (SEM) observations. Preparatory methods for the SEM included placing the peels on aluminum stubs, situating the stubs with the peels in a vacuum, and coating the entire peel with a layer of gold about 150 Å thick. The specimens were then placed in the chamber of a Cambridge Stereoscan 100 SEM, observed from 300 to 800×, and microphotographed at about 300×.

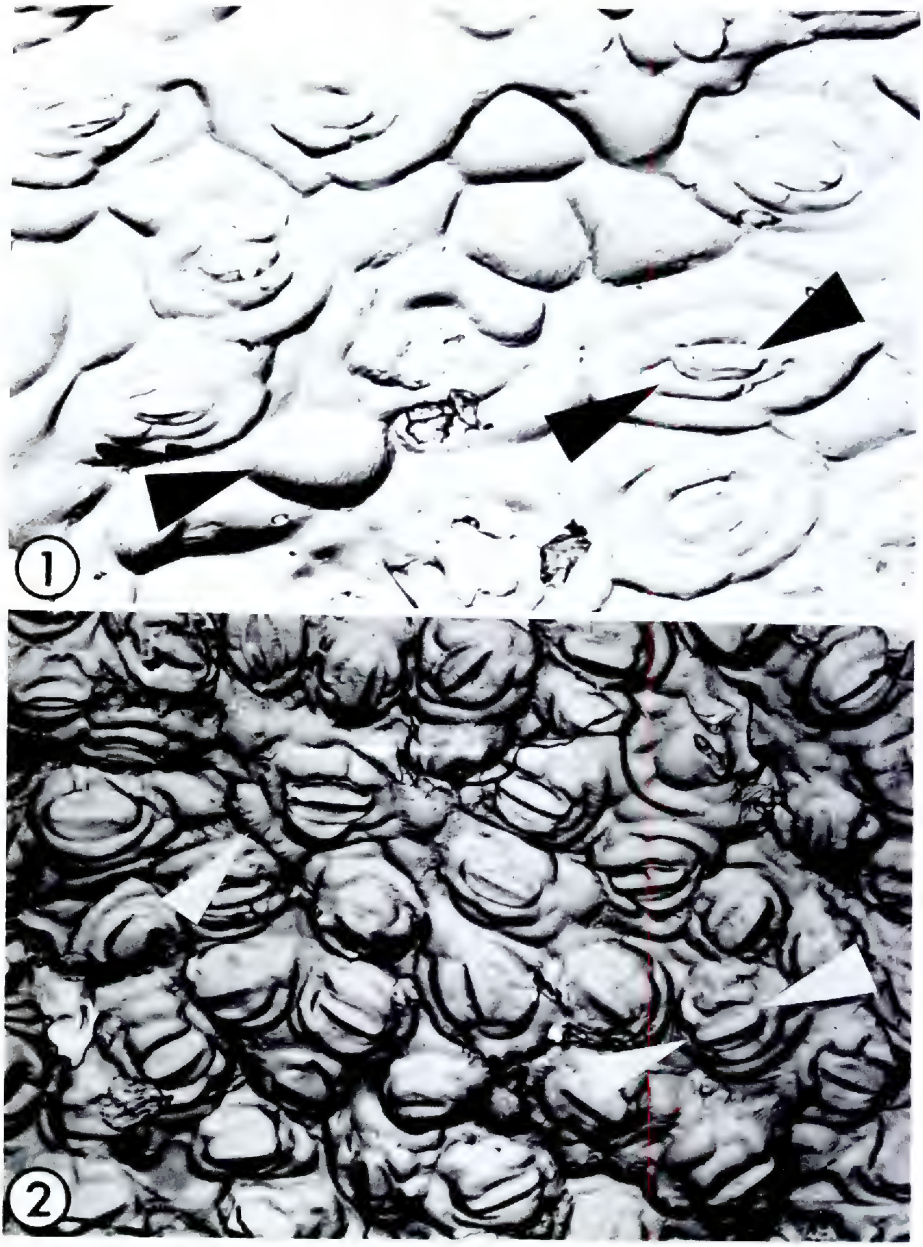
RESULTS AND DISCUSSION

The mean stomatal density for the Baños population of *Begonia parviflora* is 179.5 ± 19.13 per mm^2, and that for the Tena population is 634.7 ± 26.20 per mm^2 (see TABLE). Data were analyzed using a *t*-test at $P \leq .01$: $T_{18} = 44.4$. FIGURES 1 and 2 illustrate the difference between the two populations. The stomatal densities for the Tena population are among the highest reported for angiosperms (Salisbury, 1927; Carpenter & Smith, 1975; Abrams, 1987). In the literature available, species reported as having higher mean stomatal density values include (in stomata per mm^2) *Quercus muehlenbergii* Englem. (986), *Q. coccinea* Muenchh. (760), *Rhus copallina* L. (731), *Acer rubrum* L. (705), *Fagus grandifolia* Ehrh. (693), *Q. rubra* L. (681), *Ligustrum vulgare* L. (680), *Q. prinus* L. (662), and *Q. sessiliflora* Salisb. (656). Stomatal-density measurements from other species of *Begonia* are very limited, although several populations each of *B. heracleifolia* Schldl. & Cham. and *B. nelumbiifolia* Schldl. & Cham. have been sampled and found to have between 50 and 90 stomata per mm^2 (Hoover, 1986).

Ranges and means for stomatal density and pore lengths for B. parviflora populations.

	NUMBER OF STOMATA/MM^2		STOMATAL-PORE LENGTH (in μm)	
LOCATION/*n*	Range	Mean	Range	Mean
Baños/10	91.7–280.0	179.5 ± 19.13*	8.0–15.0	10.4 ± 0.47
Tena/10	530.0–741.8	634.7 ± 26.20	6.0–22.0	8.4 ± 0.21

*Variance is measured as the standard error of the mean.



FIGURES 1, 2. Scanning electron micrographs of *Begonia parviflora*, abaxial epidermal surfaces: 1, Baños population, × 330; 2, Puyo population, × 405. (Arrows, left to right: epidermal cell, subsidiary cell, guard cell (raised in FIGURE 2)).

The stomata of the leaves from the Tena population seem to be raised above the plane of the epidermal cells (see FIGURE 2), and the guard cells appear to sit on the apex of individual cellular protrusions that are built up on subsidiary cells. Raised stomata have been observed in other species of *Begonia*, including

B. cathayana Hemsley, *B. froebelii* A. DC., *B. lobulata* A. DC., and *B. vitifolia* Schott (Brouillet, unpublished data). In general this is an uncommon characteristic in the plant kingdom, although it has also been reported in several other genera including *Pastinaca* L., *Prunus* L., and *Solanum* L. (Esau, 1965). The stomata of the leaves from the Baños population do not appear to have this structural modification; here subsidiary cells surround guard cells in the typical way (FIGURE 1).

In the leaves from the Tena population, compared to those from the Baños population, the epidermal cells are nearly indistinguishable from the subsidiary cells (see FIGURES 1, 2); they are greatly reduced in size and appear to be localized to depressions between the stomata. The stomata, with their associated subsidiary cells, are so densely packed that the epidermal cells on the surface are the same size as the subsidiary cells.

The mean stomatal length is 10.4 $\pm$ .47 μm for the leaves of the Baños population and 8.4 $\pm$ .21 μm for those of the Tena population, a statistically significant difference ($T_{18} = 3.83$ ($p \leq .01$)). Length of the stomatal pores has been measured in many different species of *Begonia* grown under cultivation, with results indicating relatively little interspecific variation in this character (Fellerer, 1892). Five different population samplings of *B. nelumbiifolia* from along an elevational gradient in Hidalgo, Mexico, indicate rather significant variation in pore length (Hoover, 1986), suggesting that this character may not be as stable as previously reported.

Rainfall along the Amazonian slope of the Andes is one of the few climatic parameters measured for this region (Schwerdtfeger, 1976). The highest annual rainfall recorded here is found at Tena, Ecuador (annual average of 6235 mm from 1965 to 1969, including the years 1968 and 1969, when accumulation totaled 8380 and 8939 mm, respectively), thus subjecting the *Begonia parviflora* population from this region to extreme moisture. Such high rainfall is unusual for the entire eastern region of the Andes, including Venezuela, Colombia, Peru, and Bolivia. At Puyo, 59 km south of Tena, rainfall averaged 4294 mm for the same years. No data are available for the region near the Baños population, although according to Schwerdtfeger (1976 p. 154) "rainfall distribution is highly variable, mainly because of the impact of relief." It is important to note that precipitation generally decreases with elevation in this region, and since Baños is 642 m higher than Tena, it likely receives less moisture and may experience somewhat of a dry season.

With only two populations sampled for *Begonia parviflora,* it is highly speculative to interpret these data from an evolutionary standpoint, even though the populations show such extreme morphological differences that they appear to represent different taxa. Limited data indicate that stomatal density increases when plants grow in exposed, sunny conditions (Jackson, 1967; Abrams, 1987, 1988). For these *B. parviflora* populations, the high-stomatal-density Tena plants were growing in an exposed, sunny habitat, while the low-stomatal-density Baños individuals grew under moderately shady conditions, thus suggesting that the high stomatal density may be of adaptive value to the exposed conditions. Although such an interpretation conforms with existing evidence, under the circumstances this interpretation may not be entirely adequate to

explain the extreme morphological difference between the populations. Accommodation on average, of over 600 stomata per mm^2, including subsidiary cells, would predictably cause compression and reduction of epidermal cells, raising guard cells above the plane of the epidermal cells and reducing pore length. It would appear that these unusual morphological characteristics may be an architectural consequence of high stomatal density resulting during early leaf development, a process in accord with Gould and Lewontin (1978), who believed that morphological evolution may, in certain instances, be determined by structural change during development. Additional expeditions are planned for Ecuador and Colombia, data from which will assist in more thoroughly describing stomatal variation in *B. parviflora* and perhaps helping clarify the evolutionary implications of this novel leaf epidermis.

ACKNOWLEDGMENTS

This work has been supported by grants from the American Begonia Society and its associated branches, and by donations from Howard and Barbara Berg, Martin Johnson, and many other A.B.S. members. I thank William Grant, of the Williams College Biology Department, for the use of the SEM, comment on the manuscript, and his understanding and help over the years. Much gratitude is extended to Marc Abrams, Luc Brouillet, Michael Loik, Bernice Schubert, and David Smith for reviewing earlier drafts of this manuscript.

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NOTES ON THE SPECIES OF SELAGINELLA FROM GUIZHOU, CHINA

PEISHAN WANG[1]

Thirty species of *Selaginella* are currently known from Guizhou Province in south-central China. A key to these species is given. Following the key are notes on species that are newly discovered in the province, previously undescribed, or otherwise in need of discussion.

Selaginella Beauv. in China has not been studied thoroughly since Alston enumerated the Chinese species in 1934. In some provinces or regions, however, the vascular flora, including *Selaginella,* has been treated; currently about 50 species of this genus are estimated to occur in China, with 30 species known from Guizhou (Kweichow) Province in the south-central part of the country.

KEY TO THE SPECIES OF SELAGINELLA IN GUIZHOU

1. Main stems erect, suberect, or scandent, or plants with densely tufted stems; plants usually rooting at base or in lower parts.
   2. Stems densely tufted or branched from base; plants xerophytic.
      3. Stems red, branched from base; lateral and median leaves directed forward. ..... 1. *S. sanguinolenta.*
      3. Stems brown, densely tufted; only median leaves directed forward. ..... 2. *S. pulvinata.*
   2. Stems not branched near base, or if branched from base plants not xerophytic.
      4. Plants at most 6 cm high; main stems more or less zigzag. ..... 3. *S. kouycheensis.*
      4. Plants much larger; main stems not zigzag.
         5. Plants over 1 m long, scandent. ..... 4. *S. helferi.*
         5. Plants generally less than 60 cm tall, not scandent.
            6. Branches pubescent.
               7. Stems terete; leaves wrinkled when dry; northern and northeastern Guizhou. ..... 5. *S. braunii.*
               7. Stems sulcate; leaves not wrinkled when dry; southern Guizhou. ..... 6. *S. flagellifera.*
            6. Branches glabrous.
               8. Leaves below branches on main stems appressed and directed upward.
                  9. Leaves near base of main stem overlapping; median leaves not white margined; lateral leaves with basiscopic margin entire. ..... 7. *S. involvens.*
                  9. Leaves near base of main stem distant; median leaves white margined; lateral leaves with basiscopic margin serrulate. ..... 8. *S. moellendorffii.*

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Journal of the Arnold Arboretum **71**: 265–270. April, 1990.

8. Leaves below branches on main stems spreading.
    10. Median leaves entire; lateral leaves entire or subentire.
        11. Plants stout; lateral leaves entire; distal part of stems black when dry. ..... 9. *S. picta.*[2]
        11. Plants delicate; lateral leaves slightly serrulate at apex; distal part of stems straw colored or brownish when dry. ..... 10. *S. delicatula.*
    10. Median and lateral leaves serrulate or ciliate.
        12. Leaves white margined. ..... 11. *S. sichuanica.*
        12. Leaves not white margined.
            13. Sporophylls dimorphic, those on upper (dorsal) side of strobilus different both in shape and size from those on lower (ventral) side.
                14. Plants up to 40 cm or more tall; stems including leaves up to 7 mm wide.
                    15. Lateral leaves with long cilia at base; median leaves acuminate. ..... 12. *S. bodinieri.*
                    15. Lateral leaves short-ciliate or serrulate at base; median leaves aristate.
                        16. Lateral leaves ovate to ovate-lanceolate; median leaves cordate at base; species of mid-montane forests (above 1400 m alt.). ..... 13. *S. labordei.*
                        16. Lateral leaves oblong-lanceolate; median leaves not cordate at base; species of low hills and valleys (below 700 m alt.). ..... 14. *S. monospora.*
                14. Plants generally less than 20 cm tall; stems including leaves up to 5 mm wide.
                    17. Median leaves cordate at base. ..... 13. *S. labordei.*
                    17. Median leaves not cordate at base.
                        18. Median leaves strongly aristate; basiscopic margin of lateral leaves entire or subentire. ..... 15. *S. effusa.*
                        18. Median leaves acuminate; lateral leaves with margin distinctly serrulate throughout. ..... 16. *S. heterostachys.*
            13. Sporophylls monomorphic.
                19. Median leaves long-aristate; lateral leaves scabrous adaxially. ... 17. *S. trachyphylla.*
                19. Median leaves acuminate to aristate; lateral leaves smooth.
                    20. Leaves serrulate; median leaves keeled. ..... 18. *S. doederleinii.*
                    20. Leaves ciliate; median leaves not keeled.

[2]This species is found in the Guangxi Zhuang Autonomous Region near the border with Guizhou; it may also grow in Guizhou.

21. Lateral leaves symmetrical or subsymmetric, with cilia only at base; valley species of southern border of province. ..... 19. *S. repanda.*
21. Lateral leaves asymmetric, with cilia from base to near middle on acroscopic margin; species of limestone areas of province. ..... 20. *S. omeiensis.*

1. Main stems creeping; rooting throughout.
   22. All leaves entire and with distinct white margin. ..... 21. *S. uncinata.*
   22. Median and lateral leaves serrulate or ciliate, with or without white margin.
      23. Median and lateral leaves serrulate.
         24. Sporophylls similar to leaves in both shape and arrangement, not forming distinct strobili. ..... 22. *S. nipponica.*
         24. Sporophylls different from leaves, forming strobili.
            25. Plants over 20 cm long; axillary leaves oblong to oblong-lanceolate, entire; strobili with 1 megasporangium; microsporangia not spherical. ..... 23. *S. remotifolia.*
            25. Plants usually less than 10 cm long; axillary leaves spreading-ovate, serrulate; strobili with more than 1 megasporangium; microsporangia spherical. ..... 24. *S. liboensis.*
      23. Median and lateral leaves ciliate.
         26. Lateral leaves white margined.
            27. Plants 5–10 cm long; leaves with long cilia around margin. ..... 25. *S. albociliata.*
            27. Plants up to 30 cm or more; leaves ciliate at base, serrulate toward apex. ..... 26. *S. gebaueriana.*
         26. Lateral leaves not white margined.
            28. Sporophylls on upper (dorsal) side of strobilus smaller than those on lower (ventral) side. ..... 27. *S. prostrata.*
            28. Sporophylls on upper (dorsal) side of strobilus larger than or nearly equal to ones on lower (ventral) side.
               29. Lateral leaves with base symmetrical, cordate. ..... 28. *S. chaetoloma.*
               29. Lateral leaves with base asymmetric, not cordate.
                  30. Leaf margin ciliate at base, denticulate toward apex; lateral leaves ovate, acute to acuminate at apex.
                     31. Median leaves ovate. ..... 29. *S. xipholepis.*
                     31. Median leaves lanceolate. ..... 30. *S. compta.*
                  30. Leaf margin densely ciliate throughout; lateral leaves falcate, acuminate at apex. ..... 31. *S. drepanophylla.*

NOTES

3. **Selaginella kouycheensis** A. Léveillé, Repert. Spec. Nov. Regni Veg. **9:** 451. 1911; Alston, Bull. Fan Mem. Inst. Biol. **5:** 290. 1934.

I have studied the type of this species *Esquirol 2158* (E) and have found Léveillé's description of it to be incorrect. Mainly, it is not a creeping species but an erect one. Individuals that I have seen are about 1–3 cm tall (Léveillé's original description indicates a height of 6 cm), and the strobili have only megaspores. The leaves and sporophylls are both serrulate, not entire.

Léveillé cited two collections in his original description of *Selaginella kouycheensis, Cavalerie 1933* and *Esquirol 2158*. Alston's (1934) citation of *Esquirol 2158* as the type can be construed as lectotypification, a designation that is accepted here. His other citation, *Cavalerie 4156* (K), as he had pointed out, is a mixed collection. There are two other species, *S. heterostachys* Baker and *S. delicatula* (Desv.) Alston (?) in addition to *S. kouycheensis*.

A specimen from Yunnan, *C. W. Wang 78983* (Meng-pung, Jenn-yeh Hsien (A)) is also *Selaginella kouycheensis*, a new record for the province.

5. **Selaginella braunii** Baker, Gard. Chron. **1867**: 1120. 1867; Alston, Bull. Fan Mem. Inst. Biol. **5**: 281. 1934. *S. hieronymi* Alderw. Bull. Jard. Bot. Buitenzorg, ser. 2. **1**: 18. 1911.

This species is known to occur only from Zhejiang, Anhui, Hubei, Sichuan, and Guizhou provinces, all located in the Changjiang River basin. From Guizhou the following recent collections can be cited: Tongren, *East Guizhou Exped. 75325* (HGAS, PE); Tongzi, *P. S. Wang 77185, 77316* (both HGAS); Songtao, *East Guizhou Exped. s.n.*, June 1975 (HGAS). However, there is reason to believe that it also grows in Yunnan Province. While studying the materials in the Harvard University herbaria (A and GH), I found a specimen, *J. Delavay 339* (Tsin-tan, Yunnan Province), that was cited by Alston (1934) as *Selaginella elephantopus* Hand.-Mazz. However, based on its pubescent stems and wrinkled leaves, it is *S. braunii*.

6. **Selaginella flagellifera** W. Bull, Cat. no. **225**: 9. 1886. *S. biformis* A. Br. ex Kuhn, Filic. Afr. 189. 1868, *nomen nudum*; A. Brown ex Kuhn, Forschungsr. Ges. **4**(6): 19. 1889; Alston, Bull. Fan Mem. Inst. Biol. **5**: 282. 1934; Philip. J. Sci. **58**: 374. 1935; Fl. Gén. Indo-Chine, **7**(2): 570, 571. 1951; Ching, Flora Hainanica **1**: 10. 1964.

This is a tropical Asian species and is at the northern limit of its range in southern Guizhou. It is similar to *Selaginella involvens* (Sw.) Spring and *S. moellendorffii* Hieron. but is easily distinguished from them by its pubescent branches. Collections from Guizhou examined are: Congjiang Xian, *East Guizhou Exped. 75228* (HGAS, PE); Anlong Xian, *Zhang & Zhang 3304* (PE).

Although Bull indicated that the species came from Fiji, Alston (1934) placed the name in the synonymy of *Selaginella biformis* and gave the range as Burma to Sumatra and Celebes.

11. **Selaginella sichuanica** H. S. Kung, Acta Bot. Yun. **3**: 252. 1981.

Recent collections from Guizhou (Fanjingshan, Jiangkou Xian, *Sino-Brit. Bot. Exped. F0673* (HGAS, PE); *Sino-Amer. Guizhou Bot. Exped. 480* (A, CAS, HGAS, PE)) constitute a new record for the province. The species was previously known only from Sichuan.

19. **Selaginella repanda** (Desv. *in* Poiret) Spring *in* Gaudich. Voy. Bonite, Bot. **1**: 329. 1846; Alston, Bull. Fan Mem. Inst. Biol. **5**: 293. 1934. *Lycopodium repandum* Desv. *in* Poiret, Encycl. suppl. **3**: 558. 1814.

One collection of this species (Guizhou: Luodian, by Hongshui River bordering Guangxi, 280 m, *P. S. Wang 76321* (HGAS)) constitutes a new record for this province.

20. **Selaginella omeiensis** Ching *in* H. S. Kung, Acta Bot. Yun. **3:** 253. 1981.

This is a common species in limestone areas of Guizhou. It is much like *Selaginella bodinieri* Hieron., only smaller in size and with uniform sporophylls. The sporophylls and size of *S. bodinieri* are variable. Possibly they are the same species, but further evidence is needed before a final decision can be made.

25. **Selaginella albociliata** P. S. Wang, sp. nov.

Habitu S. chaetolomae Alston, sed in foliis albo-marginatis, ciliis foliorum longioribus densioribus, differt.

Plant 5–10 cm long; stem prostrate, creeping, ca. 3 mm in diameter including leaves, sparingly branched, rooting throughout. Vegetative leaves dimorphous: lateral leaves patent, ovate-oblong, 1.5–2 mm long, 1–1.3 mm wide, round at base and blunt or acute at apex, the margin white, with numerous long cilia, these patent or ascending, up to 0.3 mm long; median leaves ovate, 1–1.3 mm long, 0.5–0.8 mm wide, round at base, aristate at apex, the margin white, with numerous long cilia. Strobili 6–10 mm long, 2–2.5 mm in diameter. Sporophylls dimorphous: larger ones on upper (dorsal) side of strobilus, oblong-lanceolate, 2–2.5 mm long, 0.7 mm wide, acuminate at apex, the margin white, ciliate; smaller ones oblong-ovate, 1.8–2 mm long, 0.7 mm wide, caudate at apex, the margin white, ciliate. Megaspores light gray; microspores tangerine colored, 30 μm in diameter, verrucate.

TYPE: Guizhou, Libo Xian, on limestone surface along the Wujia River, 530 m, 20 May 1988, *P. S. Wang 77981* (holotype, HGAS).

ADDITIONAL SPECIMENS EXAMINED. GUIZHOU: Libo Xian, in soil on wet rock surface in forest, 660 m, *P. S. Wang 76801* (CDBI, HGAS).

26. **Selaginella gebaueriana** Hand.-Mazz. Symb. Sin. **6:** 9. 1929; Alston, Bull. Fan Mem. Inst. Biol. **5:** 274. 1934.

Alston (1934) listed this as a synonym of the earlier-published *Selaginella davidii* Franchet. Kung (1981) stated that the two taxa are distinct and that *S. gebaueriana* is mainly from southwestern China, while *S. davidii* is from northern China. In its larger shoots and ciliate leaves, *S. gebaueriana* may easily differ from the northern species; consequently, I agree with Kung.

28. **Selaginella chaetoloma** Alston, J. Bot. **70:** 67. 1932; Bull. Fan Mem. Inst. Biol. **5:** 292. 1934.

After studying types of *Selaginella chaetoloma* (*Cavalerie 731* (BM, E)) and additional specimens (*Cavalerie 285* (K), *517* (K), and *1469* (E)), I find that *S. prostrata* H. S. Kung (Kung, 1981) does not differ significantly, except in the

sporophylls, from *S. chaetoloma.* In *S. chaetoloma* the sporophylls on the lower (ventral) side of the strobilus are smaller than those on the upper (dorsal) side; in *S. prostrata* the opposite is true.

Alston (1932) cited specimens of *Cavalerie 731* at both BM and E as types in the original description but did not designate either as holotype. I hereby designate the specimen at BM, the more complete specimen of the two, as the lectotype.

31. **Selaginella drepanophylla** Alston, J. Bot. **70:** 66. 1932; Bull. Fan Mem. Inst. Biol. **5:** 292. 1934.

I record here a second report for the species in China (Guizhou: Fanjingshan, Jiangkou Xian, *Sino-Amer. Guizhou Bot. Exped. 68, 116, 367* (all A, HGAS, PE)). The type locality is in Guangxi, south of Guizhou. Alston (1934) pointed out that *Selaginella xipholepis* Baker, *S. drepanophylla,* and *S. compta* Hand.-Mazz. may be different forms of a single species. Recently, Dahlen (1988) treated *S. drepanophylla* as a synonym of *S. xipholepis.* After comparing the type of *S. xipholepis* with *S. drepanophylla* from Guizhou, I believe that they are very similar but separable species. *Selaginella compta* is also very similar to *S. xipholepis,* but additional specimens—especially those from Yunnan—should be checked before a decision is made on the status of these two taxa.

ACKNOWLEDGMENTS

I am grateful to the Royal Botanic Garden, Edinburgh, the Royal Botanic Gardens, Kew, and the British Museum (Natural History) for the loan of types of *Selaginella.* The staff of the Harvard University Herbaria provided the opportunity for me to study, and the Arnold Arboretum of Harvard University gave me financial support. I wish to express my special thanks to Drs. Alice R. and Rolla M. Tryon for their guidance and advice, and to Dr. David E. Boufford for his assistance in consulting literature and reading the manuscript. Professor H. S. Kung, from the Chengdu Institute of Biology, Academia Sinica, has generously helped me with specimen identificaiton and taxonomic problems on *Selaginella* during the recent years.

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KUNG, H. S. 1981. Contributions to the genus *Selaginella* Beauv. from Sichuan. Acta Bot. Yun. **3:** 251–256.

BOOK REVIEW

Genera Graminum, by W. D. Clayton and S. A. Renvoize. Kew Bulletin Additional Series XIII. Her Majesty's Stationery Office, London. 1986. 389 pp. ISBN 0-11-250006-4. £25.00 softcover.

Grass Genera of the World, by L. Watson and M. D. Dallwitz. Australian National University, Research School of Biological Sciences, Canberra. 1988. 45 pp., 5 microfiche, and 3 5.25″ disks. ISBN 0-7315-0326-0. A$40.00 softcover.

Grass taxonomy underwent a revolution in the mid-twentieth century, as anatomical and cytological data were incorporated into tribal and subfamilial classifications. Since that time, more and more data have accumulated, particularly on anatomical characters, and an integrated worldwide treatment of the family has become not only possible but highly desirable. These two publications appeared nearly simultaneously, with early versions of the Watson and Dallwitz work appearing in 1985 and 1986. They are reviewed together here because they reflect quite different approaches to the same end.

The *Genera Graminum* represents a classical treatment of the family. It is a compact book, well laid-out and easy to use. The book is divided into two parts: Part I, The Grass Plant, includes sections on morphology, reproduction, anatomy and metabolism, classification, grasslands, and evolution, as well as a brief introduction to the descriptive treatment; Part II is an enumeration of the genera, preceded by a key to the tribes. The synonymy for each subfamily, tribe, and genus is presented, followed by a diagnostic description. One of the great strengths of the book is the nomenclature, which is detailed, complete, and with typification, and will serve as a valuable aid for future taxonomic work on the group. Clayton and Renvoize recognize six subfamilies, a welcome relief for American agrostologists, whose major source for keys has been A. S. Hitchcock's *Manual of the Grasses of the United States,* which uses Robert Brown's original division into only two subfamilies.

The characters used by Clayton and Renvoize are primarily those of gross morphology: habit, inflorescence, spikelet, and floret characters. The "modern" (i.e., micromorphological) characters are given short shrift. Anatomical characters are summarized briefly for each tribe, but there is no way of assessing infratribal variation, even though this is known to be considerable in some tribes (e.g., the Paniceae, which contains both C_3 and C_4 members, members with single and with double bundle sheaths, members with each of the three known decarboxylating enzymes, etc.). This means that using the Clayton and Renvoize treatment for any other analyses is virtually impossible.

A diagram of relationships is presented for the genera of each tribe, and these are already becoming widely used, in part because they are complete. Clayton and Renvoize (p. 23) issue the disclaimer that "the diagrams are intended to

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Journal of the Arnold Arboretum **71**: 271–273. April, 1990.

give a visual impression of phenetic relationships, progressing from simple to complex structures; they obviously have phylogenetic implications, but no attempt has been made to treat these rigorously." Unfortunately, I have seen these diagrams used in presentations by agrostologists as if they were phylogenetic. This is the classic problem with nonphylogenetic descriptions of "relationships": authors may know the limitations of their work, but readers persist in interpreting relationships phylogenetically.

I find that the greatest weakness of the book is unfortunately in the rationale for statements of similarity. For example, *Cryptochloa* (Bambusoideae) is said to be "linked to *Olyra* through *O. longifolia*" (p. 63), or *Wangenheimia* (Pooideae) is "related to *Vulpia pectinella*" (p. 97). There is no evidence given for any such statements, and the diagnostic descriptions rarely provide enough information for this reader to make the comparison for herself. This means that anyone who wants to use those observations as the basis for further work must reinvent the wheel—reexamine the specimens, reevaluate the characters, and try to guess the basis for Clayton and Renvoize's assertion—before building on the observations.

Watson and Dallwitz (whose early works are curiously not cited by Clayton and Renvoize) have summarized current knowledge of the genera of the grasses in the form of an automated database. Their publication is thus only 45 pages long and is simply a set of good-quality photographs illustrating the characters used in the descriptions. The generic descriptions themselves are in the microfiche appended to the book. In addition, the publication comes with three floppy disks containing the database and the interactive program INTKEY (an MS-DOS program), used to access the information. The descriptions in the microfiche are complete and parallel, with the majority of the 430 characters described for most of the 761 genera. Characters are both macro- and micromorphological, and include geographic distribution and number of species. Synonymy is included for each genus, but it is not as detailed as that in Clayton and Renvoize; type species, for example, are not cited.

INTKEY is Dallwitz's development of Pankhurst's ONLINE and is one component of DELTA (the Descriptive Language for Taxonomy), a set of programs written by M. Dallwitz and T. Paine for creating and manipulating a taxonomic database. It functions as a multiple-entry key, thus obviating the need for any other keys in the publication. It is extremely easy to use. Because the database contains so many characters (including geography), identification can be performed rapidly with only fragmentary specimens and frequently without necessitating a lot of detailed knowledge of grass morphology. This is particularly important for a family like the Gramineae, regarded by many botanists as abstruse; identifications can easily be done by nonspecialists.

The database, used in conjunction with INTKEY, is a powerful tool with many helpful features that add up to tremendous flexibility. As one example, it keeps track of which characters are not recorded for particular genera, so the user can distinguish between the character states "not present" and "not known." This is important not only for data analyses, but also as a guide to how well sampled a character is in general, something that is impossible with the diagnostic descriptions of Clayton and Renvoize. Another detail that I have used

extensively in cladistic studies of the family is the ability to choose any set of taxa (e.g., Pooideae of North America) and to summarize the variation within the group for each character. Thus, for example, for character 18 (culm internodes solid or hollow), a single command will be able to tell you that for the particular set of 75 genera, 64 have information on the character, eight have solid stems, and 62 have hollow stems (the fact that the numbers sum to more than 64 indicates that six genera have both hollow- and solid-stemmed species).

I could go on for some paragraphs describing the many useful aspects of the grass database plus INTKEY. Suffice it to say that I have found nothing in book form to compare with it. The data are highly manipulable and are easily updated and corrected. The database contains data amalgamated from the literature and from observations made by Watson and his colleagues. The parts relying heavily on literature surveys can be unreliable, but as the data are used by more and more people for more and more purposes, errors are gradually being corrected. Updating the database is an ongoing process.

Watson and Dallwitz have not included any speculation on the evolutionary history of the family; their classification is the result of a set of phenetic analyses, and the listing of genera assigned to each tribe is printed on the microfiche and also included in the database itself. The classification is not particularly finely resolved, and there is no discussion of possible sister-group relationships—nor indeed of any relationships below the tribal level. This is reasonable in that the authors see the database as a general-purpose tool, to be available for many different sorts of evolutionary and taxonomic studies.

It is an unfortunate characteristic of systematists that more-detailed classifications are preferred over less-resolved ones, even if there is little support for the relationships implied by the detailed classifications. Thus, Clayton and Renvoize are already widely cited for their statements of relationship despite the fact that, as pointed out above, the reasons for these are largely undocumented. It seems that many workers are happy to be able to turn to a book, lift out a diagram, and assume that the relationships illustrated are accurate. The classification provided by Watson and Dallwitz, in fact, goes about as far as the available data allow; for example, neither phenetic nor cladistic analysis of the available data supports tribal divisions in the Chloridoideae, except for the well-marked Pappophoreae and Triodieae.

To conclude, I have found the Watson and Dallwitz publication to be by far the more flexible of the two, and it gives a much better understanding of character distributions. I find its only serious limitation is that some institutions (mine included) do not have appropriate computer hardware in convenient proximity to their grass collection, so the tremendous flexibility of the automated approach is outweighed by the necessity of moving the specimens to the computer. But if one is interested in identifying grasses, or in any sort of data analysis or manipulation, it is clearly the publication of choice. However, for quick reference in the absence of a computer, and for the typification of generic names, I use Clayton and Renvoize. Any herbarium and any agrostologist will probably want to own both of these. Given the total price, it is hard to resist the combination.—E. A. Kellogg, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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JOURNAL OF THE ARNOLD ARBORETUM

HARVARD UNIVERSITY VOLUME 71 NUMBER 3

ISSN 0004–2625

Journal of the Arnold Arboretum

The *Journal of the Arnold Arboretum* (ISSN 0004-2625) is published quarterly in January, April, July, and October for $70.00 per year, plus $10.00 or $15.00 postage for addresses outside of the United States, by the Arnold Arboretum of Harvard University. It is printed and distributed by Allen Press, Inc., 1041 New Hampshire Street, Lawrence, Kansas 66044. Second-class postage paid at Lawrence, Kansas. POSTMASTER: send address changes to *Journal of the Arnold Arboretum*, % Allen Press, Inc., P.O. Box 368, Lawrence, Kansas 66044.

Because publication of the *Journal of the Arnold Arboretum* is being suspended after Volume 71 (1990) has been completed, subscriptions can only be accepted for the present volume. Remittances for Volume 71 should be sent to *Journal of the Arnold Arboretum*, 1041 New Hampshire Street, Lawrence, Kansas 66044, U.S.A. Claims will not be accepted after six months from the date of issue.

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COVER: The stylized design appearing on the Journal and the offprints was drawn by Karen Stoutsenberger.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 71 JULY 1990 NUMBER 3

THE GENERA OF CUPRESSACEAE (INCLUDING TAXODIACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

JEFFREY A. HART[2] AND ROBERT A. PRICE[3]

CUPRESSACEAE Bartling, Ord. Nat. Pl. 90, 95. 1830, "Cupressinae," nom. cons.

(CYPRESS FAMILY)

Aromatic, resinous, evergreen or sometimes winter-deciduous, monoecious (or dioecious in *Juniperus* [and *Diselma*]) trees or shrubs. Bark fibrous and

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible through the support of National Science Foundation Grants BSR-8415769 (C. E. Wood, Jr., principal investigator) and BSR-8716834 (N. G. Miller, principal investigator), under both of which this account was prepared. The 133rd in the series, this paper follows the format established in the first one (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ]. The references that we have not verified are marked with asterisks.

We thank Carroll Wood and Norton Miller for the opportunities afforded by participation in the Generic Flora project and for their guidance in the study, and Rudolf Schmid for bibliographic assistance. Walter Judd and Richard Wunderlin provided useful information on the occurrence of *Callitris* in Florida. Library and herbarium collections at Harvard University and the University of California, Berkeley, were consulted in this study, and we wish to thank the staff at these institutions for their assistance. The illustration of *Chamaecyparis thyoides* (based on plants collected in Norfolk Co., Massachusetts) was drawn by Karen Stoutsenberger under the direction of Carroll Wood, while that of *Juniperus* (based on cultivated plants from the University of California Botanical Garden, and *Demaree 23779, Krivda 67-310,* and *McCabe 416,* all at UC) was drawn by Linda Vorobik under the direction of Robert Price.

This paper is published in part as contribution number 640 from the New York State Science Service.

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separating into long strips or exfoliating in plates. Wood with axial parenchyma, lacking resin canals [sometimes with traumatic resin canals in *Sequoia* and related genera] and ray tracheids [reported only for *Chamaecyparis nootkatensis*]. Branches erect or spreading; branchlets erect to pendulous, terete or quadrangular, sometimes flattened in frondlike horizontal sprays (in Cupressaceae *s.s.*). Foliage leaves entire to minutely serrate, linear to linear-lanceolate and spirally arranged (often apparently 2-ranked by twisting of leaf bases) [or opposite in *Metasequoia*] in the traditional Taxodiaceae, or decussately opposite or in whorls of 3 [rarely 4] and scalelike or sometimes awl or needle shaped in the Cupressaceae *s. s.*; foliar resin canals 1 [to 3]. Pollen cones (microsporangiate strobili) sessile or short stalked, solitary or variously clustered, terminal on leafy branches or short shoots (or sometimes axillary); microsporophylls spirally arranged, decussately opposite, or ternate, ca. 6 to 24 per strobilus; microsporangia 2 to 10 per sporophyll, globose or ellipsoid, longitudinally dehiscent, pendulous, free, in 1 or 2 abaxial rows; pollen spheroidal, without saccae or prothallial cells; intine thick, exine with surface microverrucate, with papilla or obscure germinal aperture; male cells approximately equal in size. Ovulate cones solitary (sometimes secondarily clustered), subglobose to ovoid [to pyramidal], terminal or axillary, maturing in 1 to 3 seasons; bract and scale components largely fused in the mature cone, with bract tip protrusive or inconspicuous; bract-scale complexes spirally arranged or decussately opposite or ternate, each with 1 to 6 [to 10, or rarely to 20 in *Cupressus*] erect [or ultimately inverted], adaxial, bottle-shaped ovules; archegonia aggregated in terminal (or lateral) complexes; scales peltate or broadly ovate to triangular-ovate or oblong, thickened or strongly flattened at maturity, imbricate or valvate, [2 to 4] 6 to ca. 20 [to 40 or more] per cone, ultimately woody and separating (or fleshy and fused into a berrylike structure in *Juniperus*). Seeds 1 to several per scale, with [1 or] 2 (or 3) lateral [or nearly terminal] wings derived from the seed coat, or wingless; seed coat varying from thin to very thick and woody, often with resin ducts; cotyledons 2 to 6 (to 9 in *Taxodium*). Chromosome number usually $2n = 22$ (occasionally 33, 44 [66 in *Sequoia sempervirens*]). (Including Taxodiaceae Warming, Haandb. Syst. Bot. ed. 2. 163. 1884; Juniperaceae Schaffner.) TYPE GENUS: *Cupressus* L.

A family of 29 genera[4] and approximately 130 to 140 species concentrated in the temperate portions of the Northern and Southern hemispheres, but with some species in boreal and austral areas and with *Juniperus procera* Hochst. extending into tropical montane areas of eastern Africa. Of the eight genera native in North America, *Chamaecyparis* Spach, *Juniperus* L., *Taxodium* Rich., and *Thuja* L. occur in the southeastern United States, while *Calocedrus* Kurz, *Cupressus* L., *Sequoia* Endl., and *Sequoiadendron* Buchh. occur only in the western part of the continent. About 16 of the genera are monotypic, although several of these had much larger ranges (and presumably greater numbers of species) in the Tertiary than they do now (Florin, 1963). The largest and most

[4]Or fewer, if one treats *Libocedrus* Endl. in the broad sense, including some or all of the segregate genera *Austrocedrus* Florin & Boutelje, *Papuacedrus* H. L. Li, and *Pilgerodendron* Florin, as was variously done by De Laubenfels (1972, 1988) and Eckenwalder (1976).

widespread genera are *Juniperus* (50 or more species) and *Cupressus* (perhaps 13 species) in the Northern Hemisphere, and *Callitris* Vent. (ca. 15 species) in the Southern Hemisphere.

Most recent treatments of the conifers have followed Pilger in recognizing seven families, with the Cupressaceae separate from the Taxodiaceae. However, many European authors (including Emberger, H. Erdtman & Norin, and Lebreton) have united these two families in the order Cupressales, and a number of authors (Eckenwalder; Hart; Price & Lowenstein) have advocated merging the two families under the earlier name Cupressaceae, as is done here. Although Pilger and subsequent authors have circumscribed families primarily on the basis of reproductive characters, especially those of the ovulate cone, the Cupressaceae and Taxodiaceae are similar in development and morphology of the bract-scale complexes (Florin, 1951) and differ primarily in phyllotaxy of leaves and cone scales. The leaves of the Cupressaceae *s.s.* are decussately opposite or whorled, while those of the Taxodiaceae are alternate (except in *Metasequoia* Miki ex Hu & Cheng, in which they are decussately opposite). The shift from spiral to decussate arrangement is hardly unique to the Cupressaceae *s.l.* Both patterns are also seen in the Taxaceae (where *Amentotaxus* Pilger has opposite leaves) and the Podocarpaceae (where *Microcachrys* J. D. Hooker has opposite leaves). The taxodiaceous genera also differ from the Cupressaceae *s.s.* in having a papilla protruding from the germinal area of the pollen grain, although this can be very obscure in some genera (G. Erdtman; Ueno, 1960a).

The two families are held together by an impressive number of morphological characters, including derived features of embryology (archegonia borne in complexes; free-nuclear mitotic divisions three or fewer in proembryogeny), palynology (pollen grains nonsaccate, lacking prothallial cells), chromosome base number ($x = 11$), and high degree of bract-scale fusion in the ovulate cone. Most genera have seeds with lateral wings derived from the seed coat (Singh, 1978), ovules are often more than two per cone scale, and microsporangia are usually more than two per sporophyll. Preliminary cladistic analyses of morphological characters (Hart) and immunological comparisons of seed proteins (Price & Lowenstein) indicate that the Cupressaceae *s.l.* are a natural group quite distinct from the other families of conifers and that the Cupressaceae *s.s.* form a monophyletic group apparently derived from within the traditional Taxodiaceae.

The Cupressaceae *s.l.* appear to be only distantly related to the other extant groups of conifers except for the monotypic *Sciadopitys* Sieb. & Zucc., Japanese umbrella pine, which has often been treated as a morphologically isolated member of the Taxodiaceae (see Eckenwalder; Liu & Su; Pilger; Sporne) or as the separate family Sciadopityaceae Hayata (Doyle & Brennan, 1971; Hart; Price & Lowenstein; Schlarbaum & Tsuchiya, 1985). *Sciadopitys* is similar to the Cupressaceae *s.l.* in having ovulate cones with substantial bract-scale fusion and several seeds per cone scale, each with two lateral wings derived from the seed coat, and nonsaccate pollen grains lacking prothallial cells. Its chromosome base number ($x = 10$) is apparently derived from that of the Cupressaceae *s.l.* by aneuploid reduction (Schlarbaum & Tsuchiya, 1985). It is unique among

conifers in having elongate "double needles"—axillary short shoots that combine features of leaf and stem in their development and morphology (Roth)—as its photosynthetic organs. It retains primitive states for embryological characters (archegonia not grouped in complexes, five sets of free-nuclear mitoses in proembryogeny—Dogra, 1980; Doyle, 1963; Liu & Su; Tahara, 1937, 1940), the derived states of which are shared by the Cupressaceae *s.l.*; it also differs in having male cells unequal in size (Tahara, 1940), pollen grains with much more prominent verrucate sculpture (Ho & Sziklai), and wood without axial parenchyma and with much larger cross-field pits (Phillips). *Sciadopitys* is very distant from the Cupressaceae *s.l.* in immunological comparisons of seed proteins (Price & Lowenstein), and it also has a long fossil record, dating back at least to the Jurassic (Florin, 1922, 1963; Manum). Thus it appears to be a well-separated sister-group of the Cupressaceae *s.l.* (Hart; Price & Lowenstein), and we treat it as the monotypic family Sciadopityaceae.

Most modern tribal and subfamilial classifications of the Cupressaceae/Taxodiaceae lineage have been devised in the context of two separate families, the Cupressaceae and the Taxodiaceae, or equivalent groups of lower rank (see, for example, Gaussen, 1967, 1968; Pilger; Pilger & Melchior; Vierhapper). The Cupressaceae *s.s.* have been divided into tribes or subfamilies in a variety of ways (compare Endlicher; Gaussen, 1968; Janchen; H. L. Li, 1953a; Moseley; Pilger). In perhaps the most widely utilized modern treatment, H. L. Li (1953a) divided the group into two subfamilies: Cupressoideae, with nine genera in the Northern Hemisphere (further divided into tribes Cupresseae, Junipereae Neger, and Thujopsideae Endl.), and Callitroideae Saxton, including the ten Southern Hemisphere genera plus *Tetraclinis* Masters in Spain and northern Africa (further divided into tribes Actinostrobeae Endl., Libocedreae H. L. Li, and Tetraclineae H. L. Li). The cupressoid genera were separated from the callitroid genera as having imbricate rather than valvate scales on the mature ovulate cones. However, the lowermost cone scales are often similar in arrangement in both groups, as was noted by De Laubenfels (1965). Moreover, the mature cone scales of *Cupressus* are nonoverlapping. The cones of the two subfamilies mostly differ in the reduced axis and usually fewer cone scales in the callitroid genera. The whorls of cone scales may be partially overlapping at the time of pollination in the Southern Hemisphere genera but come to lie at approximately the same level in the mature cone, rather than being separated along the cone axis. Reduction in cone-scale number has also occurred in several Northern Hemisphere genera (e.g., in *Microbiota* Komarov, with only two to four cone scales on a reduced axis (Krüssmann; Rushforth), in *Calocedrus,* and within *Chamaecyparis* and *Juniperus*). The presence of derived features of embryology (laterally positioned archegonial complexes and reduction of the number of free-nuclear divisions in the early proembryo) appears to support a close relationship among at least some of the Southern Hemisphere genera (*Callitris, Actinostrobus* Miq., and *Widdringtonia* Endl.—Dogra, 1984; Doyle & Brennan, 1972; Singh), although sampling has been very limited, and many of these genera have never been studied.

Other classifications have associated *Libocedrus* and its segregate genera with the thujoid genera of the Northern Hemisphere, which share elongate cone

scales and flattened ultimate branch systems (De Laubenfels, 1953, 1988; Janchen; Pilger; Vierhapper). However, the northern genera appear to differ in wood anatomy (Boutelje; Peirce, 1937). Distribution of tropolone and biflavonoid compounds (H. Erdtman & Norin; Gadek & Quinn, 1985), and preliminary data on anatomical characters such as details of pitting of the foliar transfusion tracheids (Gadek & Quinn, 1988) only partially agree with H. L. Li's (1953a) classification. Thus several recent authors (De Laubenfels, 1988; Gadek & Quinn, 1985, 1988) have questioned whether Li's subfamilies are natural groups, and additional morphological and macromolecular comparisons will be necessary to resolve their phylogenetic relationships.

The nine taxodiaceous genera (with *Sciadopitys* excluded) comprise only about 12 or 13 species and represent remnants of a group that was larger and more widespread in the Mesozoic and Tertiary (Florin, 1963; Miller, 1977, 1988). Many of the extant genera had wider geographic distributions in the past, as is indicated by the fossil record, and several occur back to the Cretaceous. One genus *Athrotaxis* D. Don, is now endemic to Tasmania, five (*Cryptomeria* D. Don, *Cunninghamia* R. Br., *Glyptostrobus* Endl., *Metasequoia,* and *Taiwania* Hayata) to eastern Asia, and three (*Sequoia, Sequoiadendron,* and *Taxodium*) to North or Central America.

Classifications of the Taxodiaceae have tended to emphasize form and development of the bract-scale complexes in the ovulate cone, but there are a number of differences in the details of the treatments (see Eckenwalder; Gaussen, 1967; Hida, 1957, 1962; Janchen; Liu & Su; Pilger & Melchior; Vierhapper), and a rigorous tribal or subfamilial treatment seems premature. Most authors group *Sequoia* with *Sequoiadendron* and *Taxodium* with *Glyptostrobus,* and recent researchers (Eckenwalder; Gaussen, 1967; Miller, 1988; Miller & Crabtree) have emphasized the similarities of *Athrotaxis, Cunninghamia,* and *Taiwania.* Preliminary cladistic analysis of a broader set of characters (Hart) and immunological comparison of seed proteins (Price & Lowenstein; Price, unpublished data) tend to support the groupings noted above, but place *Athrotaxis* in a more isolated position. These analyses differ primarily in the placement of *Metasequoia* and *Cryptomeria* relative to the other genera, associating *Metasequoia* with the other winter-deciduous genera *Glyptostrobus* and *Taxodium* (Hart) or with *Sequoia* and *Sequoiadendron* (Price & Lowenstein), and *Cryptomeria* with *Taiwania* and *Cunninghamia* (Hart) or with *Glyptostrobus* and *Taxodium* (Price & Lowenstein).

Chromosome numbers are often very stable within families of conifers (Ehrendorfer; Khoshoo, 1961), in marked contrast to the situation in the angiosperms. With the removal of *Sciadopitys* to its own family, the genera of Cupressaceae *s.l.* are apparently all characterized by a base number of $x = 11$.[5] Counts have been obtained for all species of the nine taxodiaceous genera and for species of 16 of the cupressaceous genera, including all ten Northern Hemisphere ones (see particularly Hair; Khoshoo, 1961; L.-C. Li; Mehra & Khoshoo; Sax & Sax). The great majority of the species have the diploid number $2n =$

[5]*Fokienia Hodginsii* (Dunn) Henry & Thomas has been reported by Chen to have a chromosome number of $2n = 24$, but L.-C. Li & Hu have more recently obtained $2n = 22$ for the species.

22. Two monotypic genera are polyploid: *Sequoia sempervirens* (Lamb.) Endl. is a hexaploid with $2n = 66$, while *Fitzroya cupressoides* (Molina) Johnston has been reported by Hair to have $2n = 44$. Triploid or tetraploid counts have been obtained for forms (primarily cultivated) of several species of *Juniperus* and also for occasional variants of the otherwise diploid *Cryptomeria japonica* (L. f.) D. Don and *Chamaecyparis pisifera* (Sieb. & Zucc.) Endl. Karyotypic comparisons of the taxodiaceous genera were reviewed by Schlarbaum & Tsuchiya (1984), who noted some differences in arm lengths and ratios and presence or position of secondary constrictions. *Cunninghamia* and *Taiwania* differ from the other taxodiaceous genera in having more diversity in chromosome size and a greater number of submetacentric (vs. metacentric) chromosomes, in agreement with the relationship between these genera indicated by their similarity in cone-scale development (Hida, 1957; Liu & Su).

The Cupressaceae *s.l.* are unusual among the conifers in having archegonia grouped tightly in complexes, usually with a well-defined jacket layer (Dogra, 1984; Liu & Su; Singh). The archegonial complexes are usually located near the micropyle, but are positioned along the sides of the gametophyte in at least some of the Southern Hemisphere genera of Cupressaceae *s.s.* (*Actinostrobus, Callitris,* and *Widdringtonia*—see Doyle & Brennan, 1972; Singh) and in *Sequoia* and *Sequoiadendron* (Liu & Su) and toward the chalazal end in *Athrotaxis* (Brennan & Doyle). There are three sets of free-nuclear mitoses in the proembryogeny of most genera, but the number is reduced to two in *Athrotaxis* and *Callitris* (and probably *Actinostrobus* and *Widdringtonia*). Wall formation accompanies the first mitotic division in *Sequoia,* a very unusual feature among the conifers (Singh). Cleavage polyembryony of various types occurs as a regular part of development in most genera of the Cupressaceae *s.l.* except for *Athrotaxis, Thuja,* and *Thujopsis,* in which it occurs only sporadically (Dogra, 1984; Doyle & Brennan, 1971, 1972).

The Cupressaceae are wind pollinated, as are the other conifers, and have a pollination-drop mechanism of pollen capture, which is seen in most other gymnosperms and is evidently the primitive state among the conifers (see Doyle, 1945; Singh). Dispersal of the seeds is usually by wind or gravity, except in *Juniperus,* where the fleshy cones are eaten by birds or mammals, and *Taxodium,* where the thickened seed coat may aid in distribution by water (Fowells).

Many taxodiaceous and cupressaceous genera have been shown to have vesicular-arbuscular mycorrhizae and to lack root nodules, while *Sciadopitys* is more similar to the Podocarpaceae and Araucariaceae in having root nodules (Khan & Valder).

Chemical studies have been conducted on wood and leaves of many of the genera of Cupressaceae *s.l.*, with greatest emphasis on the Northern Hemisphere and Australian groups (see reviews in H. Erdtman & Norin; Hegnauer, 1962, 1986). Biflavonoid composition has been studied in virtually all of the genera worldwide (Gadek & Quinn, 1983, 1985; Geiger & Quinn, 1975, 1982). Compounds of the amentoflavone and hinokiflavone series are widespread among gymnosperms generally and have been found in most genera of the family, although the latter series is apparently absent in the Australian genera *Callitris*

and *Actinostrobus* (Gadek & Quinn, 1983). The cupressuflavone series is of more limited distribution, occurring in the Araucariaceae, one genus of the Podocarpaceae (*Lepidothamnus* Phil.), and portions of the Cupressaceae *s.s.* (Gadek & Quinn, 1985; Geiger & Quinn, 1982). Cupressuflavone is a major component in *Calocedrus, Cupressus, Juniperus,* and *Tetraclinis,* and a lesser one in *Platycladus* Spach and individual species of *Chamaecyparis* and *Thuja* (but not others), all of these indigenous to the Northern Hemisphere. Taiwaniaflavone, an unusual biapigenin biflavoid found only in *Taiwania, Calocedrus,* and *Neocallitropsis* Florin, is probably a convergent feature, since the three genera are very dissimilar in morphology.

The cytotoxic lignans podophyllotoxin and/or desoxypodophyllotoxin, which have been used in both traditional and modern medicine as antitumor agents, are found in the leaves of a variety of cupressaceous genera, including *Austrocedrus, Callitris, Calocedrus, Chamaecyparis, Juniperus,* and *Thujopsis* (Cairnes *et al.*; H. Erdtman & Norin; Hegnauer, 1986). The related but noncytotoxic compound savinin is present in the wood of several species of *Juniperus* and also in *Taiwania* (H. Erdtman & Norin; Hegnauer, 1986).

Diverse terpene compounds are found in the wood, leaves, and other plant parts of the Cupressaceae *s.l.* and are responsible for much of the aromatic nature of the plants. Most of the monoterpene compounds in the Cupressaceae *s.l.* occur widely in other conifers, while sesquiterpenes of the cedrane, thujopsane, widdrane, and cuparane types are particularly characteristic of the Northern Hemisphere genera of Cupressaceae *s.s.* and also of *Widdringtonia* (H. Erdtman & Norin). Several of these compounds have recently been reported to occur in low concentration in the foliar resin of *Cryptomeria* (Yatagai & Sato), and detailed studies may find them to be more widely distributed among the taxodiaceous genera.

Tropolones structurally related to the terpenes are important heartwood components of several genera of the Cupressaceae *s.s.*, particularly those of the Northern Hemisphere. These compounds, notable for their fungicidal activity, are apparently absent from the other conifers (H. Erdtman & Norin; Hegnauer, 1986). Tropolones are characteristic of *Calocedrus, Cupressus, Platycladus, Tetraclinis, Thuja, Thujopsis,* and most but not all species of *Chamaecyparis* and *Juniperus* (H. Erdtman & Norin). They are found in *Austrocedrus* and the related *Papuacedrus* but are apparently absent in the other Southern Hemisphere genera.

Alkaloids are relatively uncommon components in the conifers and in the Cupressaceae *s.l.* are well documented only for *Athrotaxis,* all species of which contain homoerythrinane compounds (Hegnauer, 1986, 1988).

Many genera of Cupressaceae *s.l.*, especially species of *Chamaecyparis, Cryptomeria, Cupressus, Juniperus, Metasequoia, Platycladus, Sequoia,* and *Thuja,* are important as ornamental trees or shrubs (L. H. Bailey; Bean; Dallimore & Jackson; Ouden & Boom; Krüssmann). *Sequoia* and *Sequoiadendron* are among the largest trees in the world and are centers of attraction in several national and state parks in California. Wood of many genera of Cupressaceae *s.l.* is resistant to insect and fungal attack and thus has been highly sought for uses requiring durability. Wood of various species of *Juniperus, Thuja,* and *Cha-*

maecyparis has been important for shingles, and that of *Sequoia* for outdoor uses such as decks and fences.

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KEY TO THE GENERA OF CUPRESSACEAE (INCLUDING TAXODIACEAE) IN THE SOUTHEASTERN UNITED STATES

General characters: *Monoecious (or dioecious) evergreen or winter-deciduous trees or shrubs; foliage leaves alternate (often appearing 2-ranked) and linear to linear-lanceolate, or opposite to whorled and needlelike, awl-shaped, or scalelike; pollen cones with spirally arranged, opposite, or whorled microsporophylls, each sporophyll with 2 to 10 globose abaxial microsporangia; pollen nonsaccate, lacking prothallial cells; ovulate cones subglobose to ovoid or oblong; bracts and ovuliferous scales strongly fused in mature cones; scales peltate to ovate or oblong, alternate or opposite or whorled, bearing 1 to 6 [to 20] erect [or inverted] adaxial ovules; archegonia clustered; seeds with 2 (or 3) lateral wings [or 1 nearly terminal one] or wingless; cotyledons 2 to 6 (to 9); chromosome base number* x *= 11.*

A. Foliage leaves alternate, linear to linear-subulate; branchlets winter deciduous. ..... 1. *Taxodium.*
A. Foliage leaves opposite or whorled, mostly reduced and scalelike; branchlets evergreen.
  B. Branchlets forming flattened sprays.
    C. Cones globose; cone scales peltate. ..... 2. *Chamaecyparis.*
    C. Cones ovoid or ellipsoid; cone scales not peltate.
      D. Branchlets flattened in horizontal plane; seeds laterally winged; immature cone scales only slightly fleshy. ..... 3. *Thuja.*
      D. Branchlets flattened in vertical plane; seeds wingless; immature cone scales very fleshy. ..... *Platycladus.*[6]
  B. Branchlets not forming flattened sprays.
    E. Cone scales less than 1 cm long, fleshy, fused into indehiscent, berrylike structures. ..... 4. *Juniperus.*
    E. Cone scales more than 1 cm long, woody at maturity, with evident borders, separating to release seeds. ..... 5. *Callitris.*

1. **Taxodium** Richard, Ann. Mus. Hist. Nat. Paris **16:** 298. 1810.

Winter-deciduous [to evergreen] trees, pyramidal to narrowly conical when young, the crown often broad in older individuals; trunk much enlarged at base, often buttressed. Bark light- to reddish-brown, fibrous, ridged, often peeling in strips. Roots horizontal, often with cone-shaped "knees" projecting from water. Branches erect or spreading; branchlets dimorphic, those near the apex of the shoot persistent and with prominent axillary buds, those lower on the shoot without evident axillary buds and deciduous; winter buds globose, scaly. Juvenile leaves linear-lanceolate, whorled or spirally arranged; adult

[6] *Platycladus orientalis* (L.) Franco, native to eastern Asia, is commonly planted in our region and may occasionally escape (Little, 1979; Small) but needs further documentation before being considered naturalized (Wunderlin, pers. comm.).

leaves spirally arranged, either 2-ranked by twisting of leaf bases, thin and linear-lanceolate, or 5- to 8-ranked, linear-subulate and keeled, closely appressed to the branches (the 2 leaf forms on the same or different trees). Pollen cones small, ovoid, in long, drooping racemes or panicles terminating the previous year's shoots; microsporophylls 6 to 10 [to 15], broadly ovate to peltate; microsporangia (2 to) 4 to 9 (or 10), globose, pendulous, in 2 rows at base of the abaxial side of the microsporophyll; pollen with evident papilla. Ovulate cones terminal on short, scaly branchlets near ends of previous year's branchlets, maturing in 1 year; immature bract-scale complexes spirally imbricate, each with (1 or) 2 (or 3) erect, bottle-shaped ovules; mature ovulate cones subglobose to somewhat ovoid; cone scales thick, woody, peltate, 4-sided, with mucronulate umbo; resin vesicles with blood-red resin prominent on interior portions of cone scale. Seeds usually 2 on the adaxial side of each cone scale, erect, attached laterally to the stalk of the scale by a large, pale hilum; seed coat thick, woody, lustrous, with 3 small, unequal corky wings; cotyledons 3 to 9. Chromosome number $2n = 22$. TYPE SPECIES: *Taxodium distichum* (L.) Rich. (Name from Greek, in allusion to the yewlike leaves of the type species.)—BALD CYPRESS, SWAMP CYPRESS.

A genus of two closely related species or perhaps a single polymorphic one, native to swampy and riverine areas of the southeastern and central United States and from extreme southern Texas south through much of Mexico to Guatemala. The genus was widespread in Europe and western North America in the Tertiary, becoming extinct in these areas with climatic deterioration in the Pliocene (Florin, 1963).

There has been considerable disagreement concerning the number of species to recognize within *Taxodium*. Britton (1926), Dallimore & Jackson, and Rehder (1940) each recognized three species (*T. distichum* Rich. (bald cypress), *T. ascendens* Brongn. (pond cypress), and *T. mucronatum* Ten. (Tule tree, Montezuma cypress), although substantial intergradation has been reported, particularly between pond and bald cypresses.

Watson (1983, 1985), after reviewing morphological, anatomical, biochemical, and cytological data, concluded that the differences between the pond and bald cypresses are minor, showing considerable overlap and being subject to environmental modification. Watson thus suggested varietal status (as var. *imbricarium* (Nutt.) Croom) for the pond cypress, and this treatment is adopted here.

Montezuma cypress is somewhat more distinct in morphology and ecology and is allopatric in distribution (reaching extreme southern Texas from Mexico and Guatemala) and is thus usually treated as the separate species *Taxodium mucronatum,* although it may be more appropriately treated as a third variety, *T. distichum* var. *mexicanum* (Carr.) Gordon. It differs in being semievergreen, retaining its annual leafy shoots until after the new shoots have leafed out in winter or spring, and being considerably less cold hardy in cultivation than the other taxa. It has sometimes been reported to have larger, more glaucous ovulate cones (Henry & McIntyre) and longer pollen-cone-bearing branches, but more thorough sampling indicates considerable overlap for these features

(Brown, 1984; Little, 1980; Martínez, 1963). The smaller branches tend to be more drooping in the Montezuma cypress, and knees are only occasionally present (Martínez, 1950, 1963). Kaieser (1953) reported that the horizontal walls of the ray parenchyma cells are thinner in the Mexican taxon, while there is little difference in the wood anatomy of the bald and pond cypresses. Isozyme electrophoresis of population samples would be very useful in assessing the degree of genetic differentiation of Montezuma cypress from the other taxa.

Taxodium distichum var. *distichum,* bald cypress, swamp cypress, $2n = 22$, is a large tree (to 50 m) with the trunk angular at the base and the leaves two-ranked on the annual branchlets. The bark is usually thin and smooth, and the knees are usually slender. *Taxodium distichum* var. *distichum* is native on the Coastal Plain from southern Delaware to Florida, west to the valley of the Devil River in Texas, and northward in the Mississippi Embayment through Louisiana and Arkansas to southeastern Missouri and Tennessee, western and northwestern Kentucky, southern Illinois, and southwestern Indiana. The species occurs in riverine swamps that are usually inundated for several months of the year and in low, saturated stream-bank habitats and wet depressions in pine barrens. It attains its largest size in the Gulf and south Atlantic coastal areas, where it tends to form pure stands in the great river swamps. The species commonly occurs with water tupelo or tupelo (*Nyssa aquatica* L., *N. sylvatica* Marsh.) and also grows in drier habitats with red maple, water ash, and sweet gum.

Taxodium distichum var. *imbricarium* (Nutt.) Croom (*T. ascendens* Brongn., *T. imbricarium* (Nutt.) Harper, *T. distichum* var. *nutans* auct., non (Aiton) Sweet), pond cypress, $2n = 22$, is a smaller tree (to ca. 25 m in height) that occurs on the Atlantic and Gulf Coastal plains from southeastern Virginia to southeastern Louisiana. Its trunk has rounded ridges, and its appressed, subulate leaves are ca. 5–12 mm long on both annual and perennial branchlets. The bark tends to be thicker and more strongly furrowed than in var. *distichum,* and the knees, if present, are short and rounded.

Watson (1983) summarized the ecological differences between the bald and pond cypresses. Pond cypress tends to grow in pine-barren ponds, often underlain by limestone, whereas bald cypress generally occurs in riverine swamps. Additionally, the habitat of the pond cypress has a decreased water flow and is more prone to drought and fire; the pH is lower, and nutrients are less available. Neufeld and Watson (1983) have suggested that the pond cypress is a recent derivative of the bald cypress that evolved in response to harshening environments along the Coastal Plain, with the smaller, closely appressed leaves helping to reduce water loss.

Taxodium has often been considered to be closely related to the East Asian genus *Glyptostrobus,* which is similar in its habitat, possession of knees, pattern of cone-scale development, relatively large number of cotyledons (averaging ca. 5 or 6), and winter-deciduous branchlets (Britton, 1926; Henry & McIntyre; Hida, 1957; Pilger & Melchior). *Metasequoia* is also similar to *Taxodium* in being winter deciduous and having the pollen cones in a racemose arrangement, and it groups with *Taxodium* and *Glyptostrobus* in Hart's preliminary cladistic analyses. In contrast, immunological comparisons of seed proteins by Price &

Lowenstein indicate that *Taxodium* is most similar to *Glyptostrobus* and *Cryptomeria* and that *Metasequoia* is most similar to *Sequoia* and *Sequoiadendron*.

Taxodium is a very distinct genus, differing from the other winter-deciduous members of the family in a number of vegetative and reproductive characters. The knees of *Glyptostrobus* are curved and bent rather than conical and erect as in *Taxodium* (Henry & McIntyre). The older perennial branchlets of *Glyptostrobus* bear scalelike leaves that remain green for several years and have rows of white stomatal dots on the surface, whereas those of *Taxodium* bear elongate linear-subulate leaves that become brown and corky in the second year. The cones of *Glyptostrobus* are pyriform and terminal on the branchlet, have scales that are elongate and imbricate at maturity and lack prominent resin pockets, and have the bract and cone-scale united at the base but free at the tip. The body of the seed is small and ovoid, bearing a single long, nearly terminal wing. In contrast, the mature cones of *Taxodium* are globose to ellipsoid, are borne laterally on the major branchlets, and have peltate scales with the edges meeting but not overlapping. The seed body is larger, much thicker walled, and three-angled, with only small, corky wings in the angles. *Metasequoia* differs from *Taxodium* in a number of features, notably in its smaller, more flattened cone scales, its opposite rather than spirally arranged leaves and cone scales, and its strongly compressed seeds that are more than two (usually five to eight) per scale, each with two lateral wings and only two cotyledons (Florin, 1952; Stebbins).

Taxodium develops three unusual structures in response to flooding: buttswells, buttresses, and knees. The term "buttswell" refers to the enlarged basal portion of the trunk, while buttresses are longitudinal ridges on the buttswell. Variation in size and shape of these structures is associated with fluctuations in exposure of the areas to air or water during the early part of the growing season, with the height of the buttresses tending to correspond to the average depth of flooding. According to Kurz & Demaree, buttress development results from the simultaneous presence of water and air, while individuals grown under permanently flooded conditions or in well-drained soils not subject to flooding fail to develop buttswells or buttresses.

The well-known "cypress knees" are usually emergent, cone-shaped structures produced as extensions of the roots and may be as tall as 3–4 m (Brown, 1984). They may arise as small swellings on the upper surfaces of shallow adventitious roots (Shaler; Whitford) or may be formed from shallow roots growing upward and then bending sharply downward, with the geniculate point becoming the "knee" (Brown & Montz). Various functions have been attributed to the knees. One suggestion has been that they act as pneumatophores ("breathing organs") that funnel oxygen into the root system (Dickeson & Brown; Mattoon; Shaler). More recent experiments have shown, however, that little if any gas exchange occurs (Kramer *et al.*), and that no stomata, lenticels, or conducting tissues are found on the surface of the knees (Brown, 1984). Other possible functions include the storage of starch, which accumulates there in significant amounts (Brown & Montz), and stabilization of the plant during severe storms (Lamborn, 1890a). Removal of the knees appears to have little adverse affect on the trees, at least over the short term (Mattoon).

Despite considerable variation in the extent of buttressing, buttswells, and knees, some authors have attempted to use these features to distinguish bald cypress from pond cypress. Watson (1983) pointed out that their magnitude appears to be ecophenically determined since they generally do not develop if the stem is not exposed to flooding; they are thus of limited taxonomic utility.

Many bald-cypress trees reach considerable size and age. One in Louisiana measured ca. 13 m in circumference and 26.7 m in height (Brown & Montz). Some individuals of Montezuma cypress also attain great size and have multiple stems at the base. At Santa Maria de Tule in Oaxaca, the famous "Tule tree" is reported to have the largest diameter of any tree (ca. 12 m), although it appears to represent three individuals that have grown together (Cronemiller; Little, 1980). This tree has been estimated to be anywhere from 1000 to 3000 years old (Krüssmann).

The wood of *Taxodium* is known for its durability in contact with soil and severe weather. The heartwood is so durable that it has been called "the wood eternal" and has been used in several types of heavy construction. The Seminole Indians in Florida have also used the wood in construction and for fenceposts, stockades, and dugout canoes. More recently, it has been valued for interior woodwork, cooperage, fence posts, and railroad ties (Little, 1980). The wood of pond cypress is purportedly heavier and stronger than that of var. *distichum* (Harper, 1902). Wood production from *T. distichum* peaked at more than one billion board feet in 1913 but has subsequently declined substantially because of heavy cutting (Mattoon; Sternitzke). In recent years second-growth bald cypress has again built up in abundance in the southeastern United States.

The resin of *Taxodium mexicanum* has been used in Mexico as a cure for wounds, ulcers, and toothaches (Henry & McIntyre).

Taxodium is of some horticultural importance in the eastern United States and Europe and is frequently planted along watercourses and farms as a windbreak in China. Cultivars of *Taxodium* are hardy as far north as Massachusetts, New York, and Michigan and grow best in deep, sandy loam with plentiful moisture and good drainage (Fowells).

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2. **Chamaecyparis** Spach, Hist. Nat. Veg. Phan. **11**: 329. 1841.

Pyramidal monoecious evergreen trees (rarely shrubs) with nodding leading shoots and a slender, spikelike crown from a thickened trunk. Branchlets slender, flattened (gradually becoming terete in later years if not shed), distichous and forming horizontal sprays. Bark reddish- [to grayish-]brown, irregularly ridged, often peeling in strips or scales. Wood soft [or hard], whitish to pinkish [to yellowish], aromatic [or not aromatic]. Leaves entire, aromatic when crushed; juvenile leaves whorled, linear-lanceolate, acuminate; adult leaves decussate, scalelike, dimorphic, the facial pair flattened, ovate to rhombic, acuminate to obtuse, with a central gland [or eglandular]; the lateral pair rounded or strongly keeled. Cones borne terminally on lateral branchlets, opening in early spring from buds formed the previous year; pollen and ovulate cones borne on separate branches. Pollen cones ovoid to oblong, quadrangular; microsporophylls ca. 8 to 12 (to 20), decussate; microsporangia 2 to 4 (to 6); pollen microverrucate, with obscure germinal aperture. Ovulate cones globose [to ellipsoid], maturing in 1 year [2 in *C. nootkatensis*], bearing 4 to 8 [rarely to 16] decussate, peltate scales; ovules bottle shaped, erect, [1 or] 2 [to 8] per scale. Maturing cones more or less erect, glaucous, ultimately red-brown. Seeds 1 or 2 [rarely to 8] per scale, ovate, with 2 broad lateral wings; cotyledons 2. Chromosome number $2n = 22$. LECTOTYPE SPECIES: *Chamaecyparis thyoides* (L.) BSP.; see Britton, N. Am. Trees, 102. 1908. (Greek name from *chamai,* on the ground, and *kyparissos,* cypress, alluding to the affinity of the genus to *Cupressus,* true cypress.)—FALSE CYPRESS, CYPRESS.

A genus of six species in North America and eastern Asia. Three species are native to eastern Asia and three (*Chamaecyparis thyoides* (L.) BSP., *C. nootkatensis* (D. Don) Spach, and *C. Lawsoniana* (A. Murray) Parl.), to North America, with the latter two restricted to the Pacific Coast region. The Asian species are *C. formosensis* Matsum. in Taiwan, *C. obtusa* (Sieb. & Zucc.) Endl. in Japan and Taiwan, and *C. pisifera* (Sieb. & Zucc.) Endl. in Japan.

Chamaecyparis is generally thought to be closely related to the widespread Northern Hemisphere genus *Cupressus* L., which also has globose cones with peltate scales, and has sometimes been treated as a subgenus or section of the latter genus. It differs in having smaller ovulate cones (ca. 6–15 vs. ca. 15–40 mm in diameter), more heavily flattened branchlets, entire (vs. minutely ciliate) foliage leaves, and a shorter reproductive cycle (usually one vs. two years until ovulate-cone maturation). A small-coned species native to China has sometimes been treated as *Chamaecyparis funebris* (Endl.) Franco, but its biflavo-

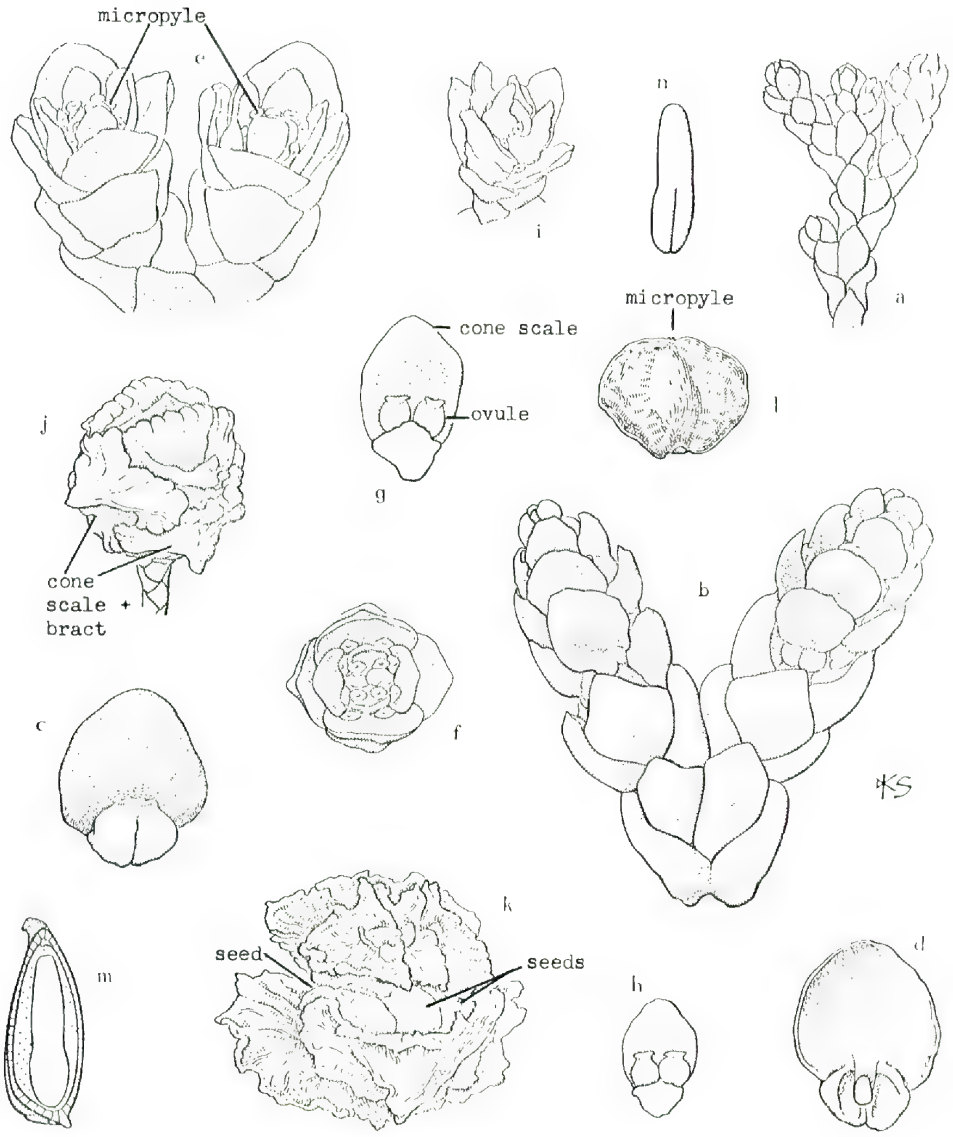

FIGURE 1. **Chamaecyparis.** a–n, *C. thyoides*: a, branchlet tip, showing lateral and facial leaves, × 5; b, detail of branchlet tip with two terminal microsporangiate strobili, × 12; c, microsporophyll with two sporangia (abaxial view), × 25; d, microsporophyll (adaxial view), showing dehisced sporangia, × 25; e, two ovulate cones at time of pollination, × 12; f, cone from "e," seen from above to show arrangement of cone scales and orthotropous ovules, × 12; g, one of lowermost pair of cone scales (adaxial view), showing two ovules at time of pollination, × 12; h, one of uppermost pair of cone scales (adaxial view) at time of pollination, × 12; i, young ovulate cone after pollination, the scales beginning to thicken and close, × 6; j, mature, unopened ovulate cone, showing fused bracts and scales, × 3; k, mature, open ovulate cone, three winged seeds visible on cone scale nearest viewer, × 5; l, winged seed, with micropyle facing upward, × 6; m, diagrammatic longitudinal section of mature seed, with embryo unshaded, gametophytic storage tissue dotted, seed coat hatched, × 10; n, embryo dissected from seed, showing two cotyledons, × 10.

noid pattern supports its original placement in *Cupressus* (Gadek & Quinn, 1987).

Chamaecyparis nootkatensis is unusual in the genus in having less-flattened branchlets and a longer reproductive cycle; it is also divergent in its biflavonoid profile and tropolone composition (H. Erdtman & Norin; Gadek & Quinn, 1985). This species also is notable for producing intergeneric hybrids with *Cupressus* in cultivation. Leyland cypress (× *Cupressocyparis Leylandii* (Jackson & Dallim.) Dallim. = *Chamaecyparis nootkatensis* × *Cupressus macrocarpa* Gordon) apparently originated in England from spontaneous crosses in both directions (Osborn). More recently, hybrids between *Chamaecyparis nootkatensis* and *Cupressus glabra* Sudw. and *C. lusitanica* Miller, respectively, have also been reported from cultivated plants in England (Mitchell).

Our sole species, *Chamaecyparis thyoides* (including *C. Henryae* H. L. Li, *C. thyoides* var. *Henryae* (H. L. Li) Little), Atlantic white cedar, white cedar, swamp cedar, "juniper," occurs in swamps and wet woods near the Atlantic and Gulf coasts from southern Maine to northern Florida and westward to southeastern Mississippi. In the northern part of its range, it often occurs in pure stands, while in the south it frequently grows with bald cypress. It can be distinguished by its adult leaves that are usually glandular and not conspicuously whitened below, and by its branchlets that are irregularly arranged rather than held in the horizontal plane. In segregating the southern populations of the species (from Florida through Mississippi) as *C. Henryae,* H. L. Li cited a number of morphological differences (e.g., smoother bark with twisting ridges, lighter-colored microsporophylls, and less-glaucous ovulate cones), but the divergence between northern and southern populations is apparently clinal rather than abrupt (Hardin; E. L. Little, 1966). Thus, E. L. Little (1966) reduced *C. Henryae* to varietal status under *C. thyoides* and later (1979) placed it in synonymy.

Chromosome counts of $2n = 22$ have been reported for four species of *Chamaecyparis* (Khoshoo, 1961; Kuo *et al.*; Sax & Sax); evidently no count has ever been made for *C. thyoides.* Natural interspecific hybridization has not been reported, but artificial crosses have been attempted in several combinations (Fukuhara; Yamamoto, 1981a, b). Meiotic irregularities have been reported in hybrids between *C. obtusa* and *C. pisifera* (Fukuhara), while a high percentage of nonviable seedlings was obtained in crosses of *C. Lawsoniana* and *C. pisifera* (Yamamoto, 1981a).

Among species of *Chamaecyparis,* significant differences have been reported in distributions of foliar terpenoids (Von Rudloff; Yatagai *et al.*) and heartwood tropolones (H. Erdtman & Norin), but more comprehensive population studies are needed. *Chamaecyparis nootkatensis* appears to be unique in the genus in having the tropolone nootkatin and the biflavonoid cupressuflavone, which are widespread in the genus *Cupressus* (H. Erdtman & Norin; Gadek & Quinn, 1985).

Most species of *Chamaecyparis* are utilized as ornamentals, with *C. Lawsoniana* (Port Orford cedar), *C. pisifera* (Sawara cypress), and *C. obtusa* (Hinoki cypress) being of particular importance. Hinoki cypress has religious significance in Japan and was often planted outside Shinto temples and used for

construction of temples and palaces (Wilson). The durable wood of the North American species has been valued for construction of boats and houses and for cooperage and shingles (Sargent, 1896, 1926). *Chamaecyparis thyoides* has historically been an important timber tree in the eastern United States, but large trees have been greatly depleted by logging (Jarvis; Tangley). Submerged logs of the species are so resistant to decay that they have been "mined" from swamps (Jarvis).

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3. **Thuja** Linnaeus, Sp. Pl. **2:** 1002. 1753; Gen. Pl. ed. 5. 435. 1754.

Evergreen, pyramidal, monoecious trees or sometimes shrubs; leading shoot erect; trunk often lobed and buttressed, sometimes dividing into 2 or more upright secondary stems. Bark reddish brown [to grayish], thin, fissured on older trees, peeling in irregular patches and fibrous shreds. Wood soft, pale, with light brown [to dark brown] aromatic heartwood. Branches horizontal at first, becoming ascendent; branchlets slender, pendulous, forming flattened, frondlike, horizontal sprays, gradually becoming terete, the smaller leafy branchlets deciduous after several seasons. Foliage fragrant; juvenile leaves in spirally arranged whorls, linear-lanceolate, acuminate, spreading or reflexed, retained on adult plants of some cultivars; adult leaves decussately opposite, scalelike, closely imbricate (except on rapidly growing shoots), the facial leaves ovate, acute tipped (to ovate-lanceolate on rapidly growing shoots), with a central gland [or eglandular], the lateral leaves folded over the facial ones, keeled. Buds small, naked, hidden by the leaves. Cones terminal and solitary, appearing in early spring; pollen and ovulate cones usually produced on dif-

ferent branchlets. Pollen cones nearly sessile, cylindrical or globose; microsporophylls ca. 4 to 6 [to 12], decussate, short stalked and more or less peltate, each with 2 to 4 microsporangia; pollen with obscure germinal aperture. Ovulate cones maturing in 1 season, terminal on short lateral branchlets, ovoid or oblong, with 8 to 12 imbricately arranged, oblong [to broadly ovate] scales, the central 4 to 6 fertile and bearing 2 (sometimes to 4) erect, bottle-shaped ovules; mature cones more or less erect; scales brownish, somewhat woody, with a minute [or more prominent] spine near the apex. Seeds (1 or) 2 (or 3) per scale, thin and flattened, with resin blisters in the thin seed coat, the membranaceous wings nearly encircling the whole seed, notched at the micropylar end; cotyledons 2. Chromosome number $2n = 22$. LECTOTYPE SPECIES: *Thuja occidentalis* L.[7] (From the Greek name of a resin-bearing conifer.)—ARBORVITAE, WHITE CEDAR.

A genus of five species, two in North America and three in Asia. *Thuja plicata* D. Don, western red cedar, is native to northwestern North America; *T. occidentalis* L. to the eastern deciduous forest area. *Thuja Standishii* (Gordon) Carr., *T. koraiensis* Nakai, and *T. sutchuensis* Franchet are native to portions of eastern Asia.

Thuja occidentalis, arborvitae, northern white cedar, white cedar, swamp cedar, $2n = 22$, is found from Nova Scotia westward to southeastern and central Manitoba, southward to the Great Lakes States and very locally south, barely reaching our region in mountainous areas of North Carolina and Tennessee. The species is common in the northern portion of its range, occurring over great areas of swampy forest land, where it forms largely impenetrable forests, as well as along rocky stream banks and drier limestone ridges, with best growth on neutral to alkaline substrates (Fernald; Fowells; Sargent, 1926). At the southern end of its distribution in western Virginia and Tennessee, arborvitae is less abundant, occurring only at higher elevations, usually on limestone or dolomitic cliffs. A number of floras (Britton, 1908; Coker & Totten; Little, 1980; Sargent, 1896, 1926) report the species from North Carolina, but there are apparently no natural populations remaining in the state (Clebsch; Radford *et al.*).

Thuja occidentalis differs from the other North American species (*T. plicata*) in usually having four rather than six fertile scales in the ovulate cone; these are also less prominently spine tipped. *Thuja plicata* is a larger tree, reaching 30–40(–70) (vs. 15–20(–25)) m in height, with more lustrous leaves that are more prominently whitened below.

The generic relationships of *Thuja* have not yet been determined with certainty. It has been suggested that it is most closely related to the monotypic eastern Asian genus *Thujopsis* Sieb. & Zucc. (Hart), which is similar in its tropolone profile (H. Erdtman & Norin) and embryogeny (Dogra, 1984) but differs in having subglobose ovulate cones with three to five (vs. usually two) seeds per scale and more spreading, hatchet-shaped lateral leaves. *Platycladus orientalis* (L.) Franco (*Biota orientalis* (L.) Endl., *Thuja orientalis* L.) has often

[7]The genus was effectively lectotypified when Spach (Hist. Nat. Veg. Phan. **11**: 333. 1841) transferred the only other Linnaean species, *Thuja orientalis,* to *Platycladus* Spach.

been treated in the genus *Thuja* and may also be closely related, but is distinct from *Thuja* and *Thujopsis* in having fleshier immature cone scales, hard-coated, unwinged seeds, regularly occurring cleavage polyembryony, and vertically rather than horizontally oriented sprays of branchlets (Dallimore & Jackson; Singh & Oberoi).

Chromosome counts of $2n = 22$ have been reported for three of the five species of *Thuja* (*T. occidentalis, T. plicata,* and *T. Standishii*) by Sax & Sax. All of the chromosomes were more or less isobranchial in a cultivar of *T. occidentalis* studied by Mehra & Khoshoo.

Several preliminary comparisons have been made of terpenoid profiles from foliage of *Thuja* species (Banthorpe *et al.*; Von Rudloff, 1975; Yatagai *et al.*). *Thuja Standishii* is quite different from *T. occidentalis* and *T. plicata* in its monoterpene profile, while *Platycladus orientalis* is apparently quite similar to the latter two species based on the preliminary data of Banthorpe and colleagues. *Thuja plicata* shows very limited variation in leaf terpenoids and isozymes (Copes; Von Rudloff & Lapp; Von Rudloff *et al.*; Yeh) and apparently went through a genetic bottleneck during Pleistocene glaciation, while *T. occidentalis* seems to be more variable at the isozyme level (Walker).

Thuja occidentalis differs from three of the other species of the genus in having cupressuflavone present in its leaves, in addition to biflavonoids of the amentoflavone and hinokiflavone series (Gadek & Quinn, 1985).

The rate and pattern of root development in *Thuja occidentalis* were found to vary in relation to swampy versus calcareous substrate (Habeck). An increased rate of stem growth and greater wood strength were also found in plants growing on relatively dry limestone substrates by Harlow.

Thuja occidentalis and *T. plicata* are valued for their light, durable wood, which has been used for construction and to make fenceposts, railroad ties, and shingles. American Indian tribes have used the thick sapwood layers of both to make woven baskets and logs of *T. plicata* to make canoes and totem poles. The bark is rich in tannin, and the leaf oil has been used medicinally. *Thuja occidentalis* was one of the first North American trees cultivated in Europe, having been planted in Paris by about 1536. It was named arborvitae (tree of life) after tea brewed from the bark (which is rich in vitamin C) saved the crew of the French explorer Jacques Cartier from scurvy (Little, 1980). Several species of *Thuja* are cultivated as ornamentals, and diverse cultivars of *T. occidentalis* have been selected (Dallimore & Jackson; Krüssmann).

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4. **Juniperus** Linnaeus, Sp. Pl. **2**: 1038. 1753; Gen. Pl. ed. 5. 461. 1754.

Dioecious (rarely monoecious), evergreen, erect to prostrate shrubs, or pyramidal to open-crowned trees. Bark reddish-brown, usually thin and scaly, falling off in longitudinal strips [rarely thick and broken into plates]. Wood fragrant, close grained, with heartwood brownish to reddish-brown. Branches spreading or upright; branchlets rounded to nearly quadrangular or triangular, grooved and somewhat flattened. Leaves aromatic, entire or minutely denticulate; juvenile leaves in whorls of 3, linear-lanceolate to subulate, spreading; leaves of mature plants either also needlelike and in whorls of 3 (having the spreading portion linear-lanceolate, with rigidly pointed apex, eglandular, entire, abscising at the juncture with the stem [or retained on the decurrent leaf base], the abaxial surface concave and grooved, with 1 or 2 whitened stomatal bands) or in sect. SABINA mainly scalelike and decussately opposite (acute to acuminate or sometimes blunt tipped, closely appressed, imbricate, entire or minutely denticulate, glandular or eglandular, firmly attached to the decurrent base). Buds naked or covered with scalelike leaves, ovate to acute. Cones axillary or terminal on short branchlets from buds of the previous autumn. Pollen cones (microsporangiate strobili) solitary [or in clusters of 3 to 6 in *J. drupacea*], ovoid to oblong; microsporophylls decussate or ternate, (6 to) 10 to 20 per cone, ovate to peltate, entire to denticulate; microsporangia (2 or) 3 to 6 [rarely to 8] per sporophyll, globose, attached to the abaxial edge of the sporophyll; pollen with obscure germinal aperture. Ovulate cones ovoid to globose, maturing in 1, 2, or 3 years, subtended by several whorls of persistent scalelike bracts, with 3 to 8 [or 9] decussate or ternate fleshy scales, these alternating with or bearing on their inner surfaces 1 or 2 [rarely 3] erect ovules; mature ovulate cones berrylike, succulent or ultimately dry and fibrous, blue, blue-black [or reddish to brownish], resinous, with scales strongly fused and their suture lines seldom evident [rarely conspicuous], obscurely or conspicuously umbonate. Seeds 1 to 3 [rarely to 14] per cone, ovoid, terete or angled, wingless, often grooved or pitted by pressure from resin vesicles in the cone; seed coat thick and bony. Cotyledons 2 [to 6]. Chromosome number $2n = 22$

(sometimes $3n = 33$ [$4n = 44$]). (Including *Sabina* Miller, *Arceuthos* Antoine & Kotschy.) LECTOTYPE SPECIES: *Juniperus communis* L.; see Britton, N. Am. Trees, 107. 1908. (Classical Latin name for juniper.)—JUNIPER, RED CEDAR.

The largest genus of Cupressaceae, with 50 or more species in North and Central America, Eurasia, and northern and eastern Africa, very widely distributed from the arctic to the mountains of the subtropics, and with one species, *Juniperus procera* Hochst., occurring on tropical mountains from 14°N to 12°S in eastern Africa (Florin, 1963). Junipers are often dominant plants in subdesert vegetation—for example, in the Great Basin area of the western United States. Of the 13 species native to the United States (Zanoni), *Juniperus Ashei* Buchh., *J. communis* L., and *J. virginiana* L. are native in the Southeast. Three sections are usually recognized in the genus, with sects. JUNIPERUS and SABINA (Miller) Spach represented by native species in our area. Section CARYOCEDRUS Endl. contains only a single species, *J. drupacea* Labill., native to Greece and Asia Minor and cultivated as an ornamental in Europe and the United States. This species, occasionally segregated in the monotypic genus *Arceuthos* Antoine & Kotschy, has very large (ca. 2–2.5 cm in diameter) and relatively woody ovulate cones with the coats of the three seeds connate, as well as clustered pollen cones, but is otherwise quite similar to sect. JUNIPERUS, having all leaves ternate and needlelike and the cones axillary.

Gaussen's (1967, 1968) informal classification treats the three sections as subgenera and divides them into ten sections (which were not formally described), largely on the bases of geography, cone color, number of seeds per cone, and presence or absence of teeth on the leaf margin. The genus has also been divided into eight informal species groups, generally following the "sections" of Gaussen, by Rushforth. Given the probability of repeated convergence for cone color and seed number, it is likely that several of the species groups in sect. SABINA are artificial, and no subsectional groups are recognized in Zanoni's treatment of the North and Central American species.

Section JUNIPERUS (sect. *Oxycedrus* Spach) (foliage leaves needlelike, ternate, eglandular, with blade jointed to the leaf base and abscising at the juncture with the stem; winter buds evident; cones solitary, axillary, with microsporophylls and cone scales ternate; ovulate cones one- to three-seeded, ripening in two or three years) comprises eight species (Dallimore & Jackson; Rushforth), primarily from northern or mountainous areas of North America, Eurasia, northern Africa, the Canary Islands, and the Azores. The only North American species is the very widespread *Juniperus communis* L. (*J. nana* Willd., nom. illeg.; *J. sibirica* Burgsd.), common juniper, ground juniper, mountain juniper, $2n = 22$, a prostrate or spreading shrub or sometimes a columnar to irregularly branched tree with a single white stomatal band generally wider than the adaxial leaf margins. It is native to much of northern North America, occurring south in the higher mountains to North and South Carolina and Georgia in the east and New Mexico and California in the west, and from coastal Greenland across Europe and northern and central Asia. Franco divided the species into four subspecies on the basis of habit and leaf morphology; he referred the eastern North American forms to subsp. *depressa* (Pursh) Franco (var. *depressa* Pursh)

because the stomatal band is narrower than the leaf margin. In our region the species is found primarily on barren rocky slopes and is a matted, prostrate shrub or very rarely a dwarfed tree (Coker & Totten).

Section Sabina Spach (adult leaves mostly scalelike and decussately opposite [or sometimes all ternate and needlelike], often with an abaxial gland, with the leaf base clearly decurrent on the stem and not jointed and abscising at the stem juncture; winter buds indistinct; cones terminal on elongating branchlets, usually solitary; ovulate cones maturing in one [or two] years, usually one- or two- [more rarely to 14-]seeded) comprises 40 or more species widely distributed in North and Central America and the Caribbean, southern and central Europe to eastern Asia, and northern and east-central Africa. The North American species have often been divided into entire- and denticulate-leaved groups (Gaussen, 1967, 1968; Hall, 1952c; Rushforth; Zanoni & Adams, 1976). The majority of them are denticulate leaved, while *Juniperus horizontalis* Moench, *J. scopulorum* Sarg., *J. virginiana*, the Mexican *J. Blancoi* Martínez, and several Caribbean species have entire scale leaves and may form a natural group (Zanoni & Adams, 1976). The denticulate-leaved species in North America tend to occur in more xeric habitats (Hall, 1952c).

Juniperus virginiana L. (*Sabina virginiana* (L.) Antoine), eastern red cedar, red cedar, savin, $2n = 22$ (rarely $3n = 33$; Stiff), is named in allusion to its red heartwood. It is very widely distributed in the eastern half of the United States and southeastern Canada. It is a tree reaching 10–15(–30) m in height, with the trunk occasionally up to 1 m in diameter. In the Atlantic States the species often occurs on dry, gravelly slopes and rocky ridges, especially on calcareous soils. In Kentucky, Tennessee, northern Alabama, and Mississippi it covers great areas of rolling limestone hills, forming nearly pure stands of small bushy trees. The "cedar glades" in the Nashville Basin of Tennessee, noted for their unusual flora (Quarterman), are dominated by the species. Eastern red cedar is also often found in abandoned fields and along fence rows. In coastal areas of the eastern Gulf States, it often grows in deep swamps (where it tends to become a large tree), as well as on coastal sands. In southwestern Texas, Arkansas, and Louisiana it attains its largest size on rich alluvial bottomlands.

The populations of the southeastern Coastal Plain (from eastern North Carolina west to southeastern Texas) have often been treated as a separate species, *Juniperus silicicola* (Small) Bailey (*Sabina silicicola* Small; *Juniperus barbadensis* auct., non L.), but detailed comparisons of morphology and terpenoid chemistry by Adams (1986) indicate that they are better treated as var. *silicicola* (Small) Silba. Varietas *silicicola* has been distinguished as having shorter scale leaves, longer pollen cones, smaller ovulate cones, and more slender twigs, but there is considerable overlap in these characters, and multivariate comparisons fail to separate the geographic groups cleanly (Adams, 1986). Multivariate comparison of terpenoid profiles gives discrete but closely adjoining inland and coastal groups. Adams noted that coastal populations tend to have cinnamon-colored rather than brownish bark and a rounded rather than pyramidal crown. On the basis of both morphology and chemistry, populations from Texas and Louisiana, previously mapped as the coastal form by Little (1971), appear to fit into var. *virginiana* better than into var. *silicicola*.

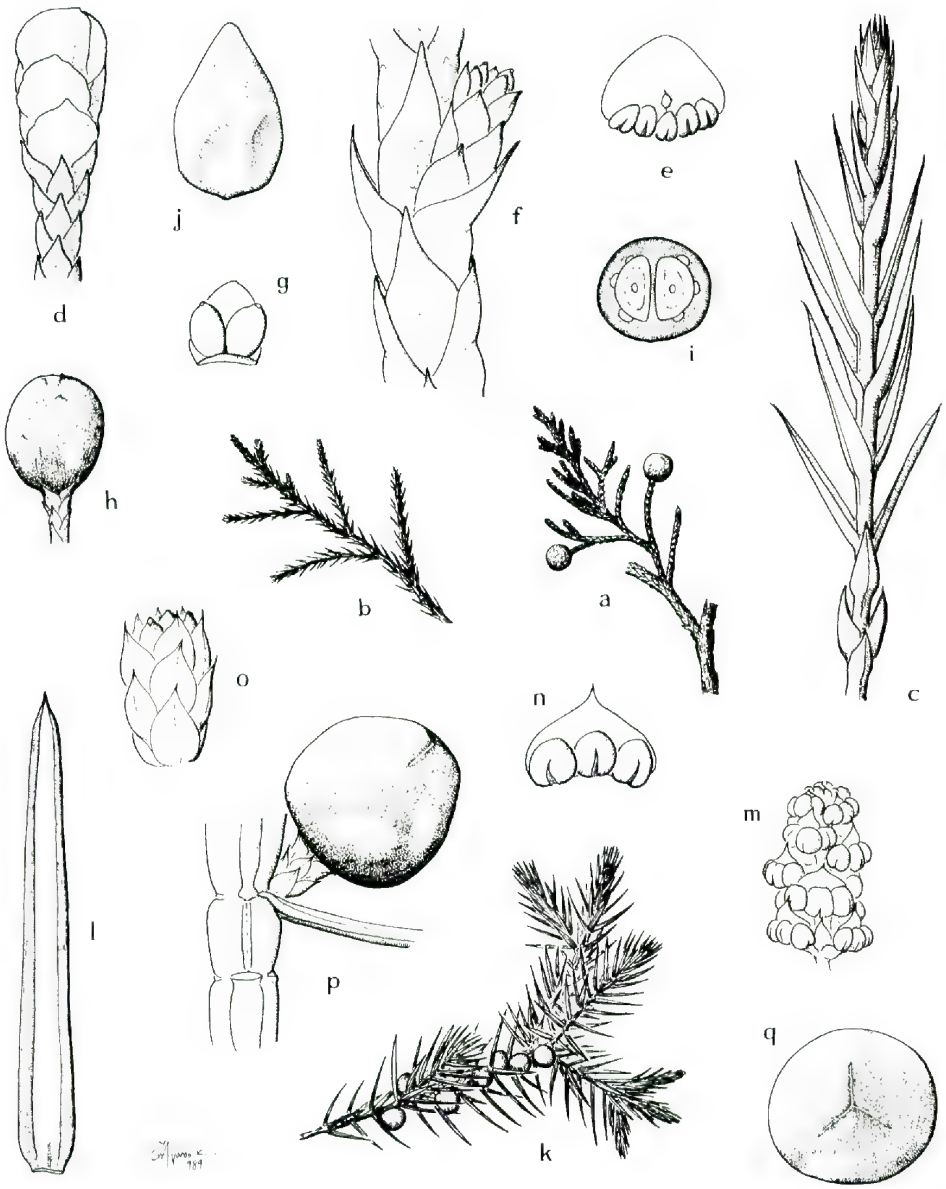

FIGURE 2. **Juniperus.** a–j, *J. virginiana*: a, branchlets with only scale leaves, bearing mature ovulate cones, × ¾; b, branchlet with scale and needle leaves, × ¾; c, detail of branchlet with needle leaves, showing decurrent leaf bases, × 5; d, microsporangiate strobilus before shedding of pollen, subtended by numerous scale leaves, × 5; e, microsporophyll (abaxial view), showing dehisced sporangia, × 10; f, branchlet with ovulate cone near time of pollination, × 7; g, cone scale (adaxial view) with 2 erect ovules near time of pollination, × 10; h, mature ovulate cone with fused cone scales, × 3; i, cross section of mature cone, only 2 seeds maturing—note resin vesicles outside seeds, × 3; j, seed, showing pits and ridges, × 5. k–q, *J. communis*: k, branch, showing ternate leaves and axillary ovulate cones, × ¾; l, detail of abscised portion of leaf in adaxial view, showing broad stomatal band, × 5; m, microsporangiate strobilus after shedding of pollen, × 5; n, microsporophyll (abaxial view), × 10; o, short axillary shoot with young

The geographic distribution of *Juniperus virginiana* adjoins or partially overlaps those of several other entire-leaved species: *J. horizontalis* to the north, *J. scopulorum* to the west, and a taxonomically complex Caribbean group of species (Adams, 1983a; Adams & Hogge; Adams, Jarvis, Slane, & Zanoni) to the south. Hybridization with *J. horizontalis* and *J. scopulorum* has been suggested on the basis of morphological variation patterns (Fassett, 1944b, 1945b; Hall, 1952c; Schurtz). Terpenoid profiles are suggestive of past introgression from *J. scopulorum* into *J. virginiana* (Adams, 1983b; Comer *et al.*; Flake, Urbatsch, & Turner). Hybridization of *J. virginiana* and *J. horizontalis* on the edge of the Driftless Area in Wisconsin has been well documented by multivariate analyses of morphology and terpenoid chemistry, as well as electrophoretic-banding patterns of peroxidase enzymes (Palma-Otal *et al.*)

Juniperus virginiana is most similar in morphology to *J. scopulorum* and the Caribbean species complex. *Juniperus scopulorum* tends to differ from *J. virginiana* and the Caribbean species in having its cones mature in the second rather than the first year. Morton noted some variation for this character in *J. scopulorum* and suggested that it be treated as a variety of *J. virginiana,* but this view has not been accepted by most later authors. Other characters that have been used to separate these species (Fassett, 1944a, b; Hall, 1952c; Rehder, 1940) include the degree of overlap of the mature scale leaves (much greater in *J. virginiana*), the width of the leaf epidermal cells (greater in *J. scopulorum*), the shape of the leaf glands (more elongate in *J. scopulorum*), and the number of sporophylls per pollen cone (lower in *J. scopulorum*), although the variation patterns are complex in both and comparisons based on wide sampling are needed. The terpenoid distribution in the two taxa is distinctly bimodal and provides support for their treatment as separate species (Adams, 1983b; Comer *et al.*; Flake, Urbatsch, & Turner), partially intergrading in the northern and southern Great Plains.

As many as six species closely related to *Juniperus virginiana* have been recognized from the islands of the Caribbean (see discussions in Adams, 1983a, 1986; Adams & Hogge; Adams, Jarvis, Slane, & Zanoni), although some authors (Dallimore & Jackson; Silba) have placed most of these taxa in synonymy under *J. barbadensis* L. *Juniperus bermudiana* L., a rare species endemic to Bermuda, differs from *J. barbadensis* and *J. virginiana* in its stouter ultimate branches, averaging 1.5 mm or more in width. Preliminary studies (Adams, 1983a; Adams & Hogge) have indicated significant differences in terpenoid distribution among some of the Caribbean taxa and between the Caribbean taxa and the morphologically similar *J. virginiana* var. *silicicola.* A detailed monographic treatment of this group is much needed.

Juniperus Ashei Buchh. (*J. mexicana* Spreng., nom. illeg.), Ashe juniper, rock cedar, mountain cedar, $2n = 22$, occurs on upland limestone or dolomite outcrops in the Ozark Mountains of northwestern Arkansas, southwestern Mis-

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ovulate cone at apex, showing 3 ovules near time of pollination, × 10; p, portion of branchlet with mature ovulate cone—note remnant leaf bases fused to larger stem, × 3; q, apical view of ovulate cone, showing suture lines between 3 fused cone scales, × 3.

souri, and adjacent Oklahoma, in the Arbuckle Mountains of southern Oklahoma, in extreme southwestern Arkansas, and more broadly in west-central Texas (where it often forms dense stands on the Edwards Plateau) and northeastern Mexico. It is a small, bushy tree differing from *J. virginiana* in its more irregular or rounded branching habit, its minutely serrulate rather than entire leaves, and its typically rounded rather than elongate leaf glands. There have been a number of reports of hybridization or morphological intergradation between *J. Ashei* and *J. virginiana* (e.g., Hall, 1952a, c; 1955), but these have not been substantiated by subsequent comparison of terpenoid profiles (Adams, 1975a, 1977; Adams & Turner; Flake, Von Rudloff, & Turner). The disjunct northern populations of *J. Ashei,* well within the distribution of *J. virginiana,* are very similar in terpenoid profiles to populations of *J. Ashei* in the main portion of its range (Adams, 1975a). *Juniperus Ashei* is apparently most similar to the Mexican species *J. saltillensis* Hall in both morphology and terpenoid patterns (Adams, 1975a, 1977; Zanoni & Adams, 1976). The terpenoids of *J. Ashei* appear to represent a subset of those in the latter species, which may be its progenitor (Adams, Von Rudloff, Zanoni, & Hogge, 1980).

Juniperus is a very distinct genus in the Cupressaceae on the basis of its unique fleshy cones with fused cone scales; it has sometimes been placed in a monogeneric tribe or subfamily. Its affinities to other genera are not well established on the basis of morphology, but the genus is similar to *Cupressus* in its distribution of tropolones (H. Erdtman & Norin) and biflavonoids (Gadek & Quinn, 1985).

Juniperus has been the subject of an increasing number of detailed taxonomic studies using multivariate analyses of terpenoid chemistry, as well as morphology (see, for example, Adams, 1983a, b, 1986; Adams & Hogge; Adams, Von Rudloff, Hogge, & Zanoni; Adams, Von Rudloff, & Hogge; Zanoni & Adams, 1975, 1976), and preliminary revisions have been presented for the Mexican and Guatemalan (Zanoni & Adams, 1979) and North American (Zanoni) taxa of sect. SABINA. Species delimitation is often very difficult in the genus, and overall monographic treatment is much needed. Problems in distinguishing species are partially due to the relatively cryptic characters of leaves, stems, cones, and seeds used to separate them and to our poor knowledge of certain species. To a large degree, however, they are due to the complexity of variation within species and the limited divergence or convergence among them. Fassett's (1944a, b; 1945a, b) work on *J. virginiana, J. horizontalis,* and *J. scopulorum* illustrates the problems in attempting to discriminate among closely related species by the use of univariate comparisons of morphological characters—problems that have been obviated in part by multivariate analysis and the use of independent chemical data sets. Fassett found that quantitative variation within individual populations can be substantial, and that characters yielding statistically significant differences among species often show a considerable degree of overlap. Zones of past or present hybridization in the areas where the species meet also add to the taxonomic complexity.

As in the rest of the family, *Juniperus* most frequently has a chromosome number of $2n = 22$. Counts have been obtained for at least 23 species (see especially Hall, Mukherjee, & Crowley, 1973, 1979; Khoshoo, 1961; Mehra;

Mehra & Khoshoo; Sax & Sax) of which 19 are reported to be diploid or preponderantly diploid. Triploid or tetraploid plants have been found predominantly in horticultural variants (e.g., in *J. chinensis* L. and *J. squamata* Buch.-Ham.); their frequency in wild populations is unclear. Some species differ in karyotype; e.g., one chromosome pair is markedly heterobrachial in *J. horizontalis* and *J. procera,* while all of the chromosomes are more or less isobrachial in *J. communis, J. virginiana,* and several other species (Mehra; Mehra & Khoshoo; Mujoo & Dhar; Ross & Duncan).

As discussed by Lemoine-Sébastian (1968), evolution within the genus *Juniperus* has been marked by repeated reductions in the numbers of both cone-scale whorls and ovules, culminating in several species with a single apparently terminal ovule enveloped by one whorl of cone scales. Seeds with very hard coats contained in fleshy, "berrylike" cones are effective adaptations for seed dispersal by birds or sometimes mammals (Holthuijzen & Sharik, 1984, 1985; Phillips). As in a number of other groups of conifers, animal dispersal of seeds is coupled with a dioecious breeding system (Givnish).

Several species of junipers (e.g., *Juniperus virginiana*) are hosts for cedar-apple rust (*Gymnosporangium* spp.), which produces conspicuous gall-like growths on the plant (illustrated in Coker & Totten) and is a serious pathogen of cultivated apples and other woody Rosaceae.

The wood of *Juniperus* is fragrant, very durable, and little damaged by insects. Wood and bark of several North American species have been found to be very effective termiticides (Adams, McDaniel, & Carter). The wood of *J. virginiana* has been much used for pencils, although incense cedar (*Calocedrus decurrens* (Torrey) Florin) is now much more widely employed for this purpose because of heavy exploitation of red cedar (Hemmerly). Red cedar wood has been widely used for fenceposts and furniture, especially moth-resistant cedar chests for storage of clothing. In the western United States junipers are also highly valued for their aromatic firewood. The essential oil (cedarwood oil) from the heartwood of *Juniperus* species has been widely utilized in compounding fragrances for soaps, perfumes, and industrial uses, as well as in microscopy as a mountant (Adams, 1987; Hemmerly). Leaf or fruit oils of *Juniperus* have been used medicinally and can possess powerful diuretic properties. Many species of junipers are grown as ornamentals, and a large number of habit and color variants have been selected, particularly in *J. chinensis, J. communis,* and *J. virginiana* (Dallimore & Jackson; Krüssmann; Ouden & Boom). Juniper "berries" from *J. communis* are used as flavoring agents in cooking and in the production of the alcoholic beverage gin (the name shortened from Dutch *jenever,* traceable back to Latin *juniperus*).

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5. **Callitris** Ventenat, Dec. Gen. Nov. 10. 1808.

Evergreen monoecious trees or shrubs with spreading or erect branches. Bark grayish, furrowed [brownish and fibrous in *C. Macleayana*]. Wood very dense, not distinctively colored. Juvenile leaves needlelike, in whorls of four; adult leaves scalelike, triangular, in whorls of 3, with bases decurrent and fused to the stem. Pollen cones solitary or clustered near branchlet tips; microsporophylls in whorls of 3 [rarely 4], each with (2 or) 3 (or 4) sporangia. Ovulate cones globose [to ovoid or conical], terminal on short, thickened stalks, bearing 6 [sometimes 8 in *C. Macleayana*] cone scales in 2 alternating and unequal whorls of 3, appearing to form a single whorl at maturity; cone scales thickened, triangular-ovate, valvate and opening out from the very reduced cone axis (columella); ovules [6 to] 18 to 36 [to 54] per cone, in 3 intersecting rows arranged around the columella and at the base of the cone scales. Seeds flattened, irregularly tetrahedral, bearing [1 or] 2 or 3 lateral wings; cotyledons 2 (rarely 3). Chromosome number $2n = 22$. (Including *Octoclinis* F. Mueller; *Frenela* Mirbel.) LECTOTYPE SPECIES: *Callitris rhomboidea* (R. Br.) A. & L. Rich.; see Bullock, Taxon **6**: 227. 1957. (From Greek *kallistos,* beautiful, and *treis,* three, in reference to the arrangement of leaves and cone scales.)—CYPRESS PINE.

A genus of approximately 15 species, 13 in Australia and two in New Caledonia. *Callitris* is divided into sect. OCTOCLINIS Bentham, including only *C. Macleayana* (F. Mueller) F. Mueller, and sect. CALLITRIS (sect. *Hexaclinis* Bentham). *Callitris Macleayana* is unusual in having some ovulate cones (those on shoots retaining the juvenile leaf type) with eight rather than six scales, both numbers often occurring on the same tree; loosely fibrous rather than dense, vertically furrowed bark; and only one elongate wing on the seed rather than two or three smaller ones (Baker & Smith; Clifford & Constantine; Garden).

Callitris columellaris F. Mueller var. *campestris* Silba (*C. glaucophylla* J. Thompson & L. Johnson; *C. glauca* R. Br. ex Baker & Smith, nom. illegit.), white cypress pine, $2n = 22$, has escaped from cultivation and has become locally naturalized in sand-pine (*Pinus clausa*) scrub in Brevard, Indian River, Orange, Osceola, and Seminole counties in eastern Florida (Judd, pers. comm.; Little, 1979; Wunderlin, pers. comm.). It is characterized by usually glaucous, unkeeled leaves and generally solitary ovulate cones with rugose but not verrucate scales that separate to near the base at maturity.

The nomenclature and species circumscription in the *Callitris columellaris* complex has been controversial. Franco chose a specimen referable to *C. columellaris* var. *columellaris* as a lectotype for *C. Hugelii,* a new combination based on *Frenela Hugelii* Carr., which would be an earlier name for the species. Blake has contended, however, that the specimen chosen was an inappropriate neotype probably representing a different species from that described in the protologue.

Several authors (Baker & Smith; Garden; Lacey; Thompson; Thompson & Johnson) have recognized three ecogeographic species in the *Callitris columellaris* complex: *C. glaucophylla* (*C. glauca*) in inland areas of the southern two thirds of Australia, *C. intratropica* Baker & Smith in the tropical zone of northern Australia, and *C. columellaris* s.s. in coastal areas of Queensland and

New South Wales. Other authors (Blake; Clifford & Constantine; Dallimore & Jackson; Venning, 1979, 1986) have emphasized morphological intergradation among these taxa, however, and they are treated here as varieties following Silba. There appear to be genetically based differences in plant habit and in foliage color and density among the three varieties (Lacey; Thompson & Johnson). In particular, the inland var. *campestris* usually has more glaucous foliage than the other varieties (hence the name "white cypress pine"), while var. *columellaris* has denser, dark green leaves and a more irregular branching pattern. Varieties *campestris* and *columellaris* are quite similar in cone size, while var. *intratropica* (Baker & Smith) Silba has been distinguished on the basis of its smaller cones (usually less than 1.8 cm wide) with narrower upper cone scales (Thompson & Johnson). It is uncertain whether plants from southern Queensland, between the generalized geographic ranges given for vars. *intratropica* and *campestris* by Thompson & Johnson, were included in the morphological comparisons (see Blake). Differences in leaf and wood chemistry among the taxa have been reported based on limited sampling (see Baker & Smith; Lacey; Thompson & Johnson), but thorough range-wide comparisons are needed to assess their validity.

The widespread south Australian species *Callitris Preissii* Miq. can also approach *C. columellaris* in morphology and leaf-oil chemistry (Adams & Simmons), and the taxa have been reported to produce fertile hybrids (Thompson & Johnson).

Chromosome counts for six species of *Callitris,* all $2n = 22$, were given by Mehra & Khoshoo. Similar karyotypes are seen in these species, with the chromosomes having median or submedian centromeres. Natural hybridization has been reported for three of these taxa, *C. Preissii, C. verrucosa* (A. Cunn. ex Endl.) F. Mueller, and *C. columellaris* var. *campestris,* in all possible combinations (Adams & Simmons; Garden; Thompson & Johnson).

Morphologically, *Callitris* shows the greatest similarity to the western Australian genus *Actinostrobus* Miq., which differs most prominently in having its ovulate cones subtended by a number of closely imbricate bracts. These are lacking in *Callitris.* Both genera have decurrent leaves in whorls of three and ovulate cones of six basally fused cone scales; they also have similar biflavonoid profiles, lacking in cupressuflavone and hinokiflavone derivatives (Gadek & Quinn, 1985). The southern African *Widdringtonia* Endl., which is similar to *Callitris* and *Actinostrobus* in embryology, differs in having decussately opposite foliage leaves, only four scales per ovulate cone, and a much more complex biflavonoid profile.

The sesquiterpene alcohol guaiol is a very characteristic component of the heartwood of *Callitris,* often crystallizing from cut stumps (Baker & Smith); within the Cupressaceae s.l. it has otherwise been reported only from the New Caledonian genus *Neocallitropsis* (H. Erdtman & Norin).

Several species of *Callitris* are important timber trees in Australia, furnishing hard, durable, termite-resistant wood for construction. The bark is rich in tannin. Resin exuding from the inner bark of cut stumps is similar to sandarac (obtained from *Tetraclinis*) and has been used in the manufacture of varnishes and incense (Lacey). In Australia various species of *Callitris* are widely planted

as windbreaks and ornamental trees and are particularly valuable for their drought resistance.

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THE PHYLOGENETIC SIGNIFICANCE OF STOMATA AND TRICHOMES IN THE LABIATAE AND VERBENACEAE

PHILIP D. CANTINO[1]

Epidermal anatomy was surveyed in leaves of 127 genera of Labiatae and 59 of Verbenaceae *sensu lato*, with emphasis on the morphology of the stomatal complexes and the minute subsessile glandular trichomes that are found in nearly all members of both families. The phylogenetic significance of the data above the genus level was analyzed, using the subfamilies of Verbenaceae as outgroups to the Labiatae, and the Scrophulariales as outgroup to the Verbenaceae. Many of the characters exhibited such a large amount of intrageneric variation that they have little value as phylogenetic indicators above the species level. In general, the presence/absence of stomatal types varied less within genera than presence/absence of glandular trichome types. Although the phylogenetic significance of these epidermal features must ultimately be evaluated in light of other characters, the derived states in parentheses suggest the existence of clades comprising the following taxa: *Brazoria, Macbridea,* and *Physostegia* (absence of anomocytic stomata); all Labiatae except the Prostanthereae and *Amethystea, Tetraclea, Tinnea,* and *Trichostema* of the Ajugeae (presence of diallelocytic stomata); *Phyla* (presence of two-armed unicellular trichomes; parallelocytic stomata); subfam. Verbenoideae, with the possible exception of four genera (absence of uniseriate "hairs" in nonglabrous species; i.e., only unicellular hairs occur); and all Chloanthoideae except *Nesogenes* (presence of branched, multicellular trichomes). The suite of stomatal types found in tribe Prostanthereae and *Tetraclea* and *Trichostema* of tribe Ajugeae differs markedly from that found in the rest of the Labiatae and resembles that in some Verbenaceae, particularly subfam. Chloanthoideae and tribe Clerodendreae. However, difficulty in assessing polarity of two of the relevant characters makes evaluation of cladistic relationships difficult.

In an earlier paper (Abu-Asab & Cantino, 1987a) the leaf anatomy of subtribe Melittidinae (Labiatae) was surveyed, and an attempt was made to evaluate the phylogenetic significance of anatomical variation in the group. This effort was hindered by a scarcity of published data on the leaf anatomy of other subgroups of the Labiatae. Assessment of character polarities within the ingroup was based on outgroup comparison, but the outgroups comprised a mere scattering of labiate genera for which anatomical data happened to be available. This is not an unusual problem since there are few comprehensive surveys of the leaf anatomy of large families.

The present survey is comprehensive to the extent that all major groups of the Labiatae and nearly all those of the Verbenaceae *sensu lato* have been

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Journal of the Arnold Arboretum **71:** 323–370. July, 1990.

included. However, the effort to maximize the breadth of the survey with regard to genera and suprageneric groups has resulted in a rather scanty sample of intrageneric variation, particularly within subfam. Nepetoideae (Labiatae). Moreover, not all aspects of epidermal anatomy were studied; emphasis was placed on those characters that Abu-Asab and Cantino (1987a) found to be of systematic significance. Despite these limitations, this survey is the only one available for the Labiatae or Verbenaceae as a whole and one of few available for a major angiosperm family. It is hoped that the data provided here will facilitate evaluation of the phylogenetic significance of leaf-epidermal variation within genera of both families.

TAXONOMIC BACKGROUND

It is widely accepted that the Labiatae evolved from the Verbenaceae (i.e., the immediate ancestors of the Labiatae, if alive today, would be assigned to the Verbenaceae). The two families form the core of the order Lamiales of Dahlgren (1980), Cronquist (1981), Thorne (1981), and Takhtajan (1986). The boundary between the Labiatae and the Verbenaceae is unclear. Traditionally, they have been distinguished on the basis of stylar position—terminal in the Verbenaceae and gynobasic in the Labiatae. However, in the members of tribes Ajugeae and Prostanthereae of the Labiatae as well as some Verbenaceae, the gynoecium is intermediate in structure, the ovary being shallowly four-lobed and the style neither terminal nor fully gynobasic. Thus the taxonomic limits of the Labiatae are unclear, and there is no discrete character state (let alone a clearly derived one) supporting its monophyly. On the contrary, pollen morphology suggests that the Labiatae may be polyphyletic, with the more primitive genera having arisen from different subgroups of the Verbenaceae (Abu-Asab & Cantino, 1987b). Consequently, if a character survey of the Labiatae is to be useful in phylogenetic inference, it should include representatives of a wide variety of Verbenaceae as well.

The classification of the Verbenaceae used here is that of Moldenke (1971), except that Cronquist's (1981) broader circumscription of the family is adopted. Thus, the segregate taxa Avicennioideae, Chloanthoideae, Nyctanthoideae, Phrymoideae, Stilboideae, and Symphorematoideae, recognized as families by Moldenke, are treated as subfamilies here. This is done for convenience of data tabulation only and is not intended as a judgment on the relative merits of familial versus subfamilial rank for these taxa. For the Labiatae Erdtman's (1945) subfamilial classification (see Cantino & Sanders, 1986) has been adopted. Within subfam. Nepetoideae Bentham's (1876) tribes are used (with corrected nomenclature of Sanders & Cantino, 1984), with the exception that those Pogostemoneae with tricolpate pollen are removed to the Lamioideae. Within subfam. Lamioideae five tribes are recognized here: Ajugeae *sensu* Bentham (1876), Prostanthereae *sensu* Bentham (1876), Lamieae *sensu* Abu-Asab and Cantino (1987a), Pogostemoneae (comprising *Colebrookea* Smith, *Comanthosphace* S. Moore, *Eusteralis* Raf., *Leucosceptrum* Smith, *Pogostemon* Desf., and *Rostrinucula* Kudo), and Scutellarieae (comprising *Scutellaria* L., *Salazaria* Torrey, and *Harlanlewisia* Epling). Although it would be simpler to adopt

Bentham's classification in its entirety, modifying it as is done here increases the proportion of the tribes for which there is evidence of monophyly. Nonetheless, certain infrafamilial taxa (designated with quotation marks in the tables) are recognized here in spite of their probable nonmonophyly because they have not yet been sufficiently studied to subdivide them in a way that better reflects phylogeny. Their use facilitates tabulation and summary of the data, but in recognition of their questionable status, their monophyletic component taxa are treated as separate units in the analysis.

MATERIALS AND METHODS

Leaf mounts were prepared from herbarium material by a procedure developed by Jon Hamer, modified from Abu-Asab and Cantino (1987a). Dried leaves were soaked overnight in a weak solution of Alconox soap in water, then transferred to five percent sodium hydroxide for twelve hours to three days, depending on leaf thickness. After being bleached in a 30 percent solution of household bleach (30 minutes to four hours, depending on the material), the leaves were placed in 50 percent ethanol for at least ten minutes, then stained with ferric tannate (2.5 percent tannic acid in 50 percent ethanol, followed by 2.5 percent ferric chloride in 50 percent ethanol; modified from Berlyn & Miksche, 1976) and mounted in surface view. A set of permanent slides is on deposit in the Bartley Herbarium of Ohio University (BHO).

The study set included representatives of 59 genera of the Verbenaceae *sensu lato* and 127 of the Labiatae. Within the latter, 69 genera of subfam. Lamioideae and 58 of subfam. Nepetoideae were included. Six additional genera of the Lamioideae and one of the Nepetoideae were examined by Abu-Asab and Cantino (1987a). When the two data sets are combined (see TABLES 1, 2), the total represents approximately 60 percent of the genera of Verbenaceae *sensu lato,* 73 percent of subfam. Lamioideae, and 36 percent of subfam. Nepetoideae (estimates of the number of genera in the Verbenaceae *sensu lato* and in the subfamilies of the Labiatae are derived from Moldenke (1971) and Cantino & Sanders (1986), respectively). A much higher proportion of the genera of the Verbenaceae and the Lamioideae were sampled than of the Nepetoideae because variation in the former groups may be particularly helpful in understanding the origin and early evolution of the Labiatae. (Subfamily Nepetoideae represents a single large clade that arose from within the paraphyletic or polyphyletic subfam. Lamioideae; see Discussion.) The list of voucher specimens was excluded from this report because of its length, but copies have been deposited in the libraries of the Harvard University Herbaria, the Missouri Botanical Garden, the New York Botanical Garden, and the United States National Herbarium. The vast majority of the specimens from which leaves were obtained are at A, BHO, and GH, but a few are at MO, NY, and US (abbreviations follow Holmgren *et al.,* 1981).

In the examination of the prepared slides, emphasis was placed on two sets of characters that Abu-Asab and Cantino (1987a) found to be of systematic significance in the Labiatae: the morphology of the stomatal complexes and the structure of the minute, subsessile glandular trichomes that are character-

TABLE 1. **Stomatal characters in Labiatae and Verbenaceae.**

Taxa[a]	Stomatal Types[b,c] ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	Stom. Pos.[d]
Lamiaceae										
"Lamioideae"										
"Ajugeae"										
Acrymia ajugiflora Prain	-	-	-	-	-	-	+	+	*	hypo
Ajuga chamaepitys (L.) Schreber	+	+	-	-	-	-	*	+	-	amph
A. genevensis L.	+	-	-	-	-	-	*	+	-	amph
A. laxmannii Benth.	+	+	-	-	-	-	*	+	-	amph
A. linearifolia Pampan.	+	+	-	-	-	-	*	+	-	amph
A. reptans L.[§]	+	+	-	-	-	-	*	+	-	amph
A. sciaphila W.W.Smith	+	+	-	-	-	-	*	+	-	amph
Amethystea coerulea L. (#1)	*	+	-	r	-	+	+	-	-	hypo
A. coerulea L. (#2)	*	+	-	-	-	+	+	-	-	hypo
Cymaria dichotoma Benth.	+	+	-	-	-	r	*	r	-	hypo
Kinostemon ningpoensis (Hemsley) Kudo	+	+	-	-	-	-	+	*	+	hypo
K. ornatum (Hemsley) Kudo (#1)	+	-	-	-	-	-	*	+	+	hypo
K. ornatum (Hemsley) Kudo (#2)	+	-	-	-	-	-	+	*	+	hypo
K. ornatum (Hemsley) Kudo (#3)	+	+	-	-	-	-	+	*	+	hypo
K. pernyi (Franchet) Kudo	r	-	-	-	-	-	+	*	+	hypo
Rubiteucris palmata (Benth. ex Hook.f.) Kudo	*	+	-	-	-	-	+	+	-	hypo
Schnabelia oligophylla Hand.-Mazz.	*	?	?	?	?	?	+	?	?	hypo
Tetraclea coulteri A.Gray (#1)	*	+	-	+	-	+	-	-	-	amph
T. coulteri A.Gray (#2)	*	+	-	+	-	+	-	-	-	amph
T. coulteri A.Gray (#3)	*	+	-	+	-	+	r	-	-	amph
Teucrium arduinii L.	*	+	-	r	-	r	+	r	-	amph
T. canadense L.[§]	+	-	-	-	-	-	*	+	-	hypo
T. chamaedrys L.[§]	+	-	-	-	-	-	*	+	-	hypo
T. integrifolium F.Muell. ex Benth.	*	-	-	+	-	+	+	r	-	amph
T. laciniatum Torrey	+	+	-	-	-	r	*	+	-	amph
T. marum L.	+	?	?	?	?	?	*	+	?	hypo
T. rotundifolium Schreber	+	-	-	-	-	-	*	+	-	amph
Tinnea aethiopica Kotschy ex Hook.f.(#1)	*	+	-	-	-	r	+	-	-	hypo
T. aethiopica Kotschy ex Hook.f. (#2)	*	+	-	-	-	-	+	-	-	hypo
T. antiscorbutica Welw.	*	+	-	-	-	-	r	-	-	hypo
T. apiculata W.Robyns & Lebrun	*	+	-	-	-	-	+	-	-	hypo
T. galpinii Briq.	*	+	-	-	-	r	+	-	-	hypo
T. rhodesiana S.Moore (#1)	*	+	-	+	-	+	+	-	-	amph
T. rhodesiana S.Moore (#2)	*	+	-	-	-	-	+	-	-	hypo
T. somalensis Gurke ex Chiov.	*	+	-	-	-	-	+	-	-	hypo
Trichostema arizonicum A.Gray (#1)	*	+	-	+	-	+	-	-	-	amph
T. arizonicum A.Gray (#2)	*	-	-	+	-	+	-	-	-	amph
T. brachiatum L.	+	?	?	*	?	?	?	?	?	amph
T. dichotomum L.[§]	+	+	-	*	-	+	-	-	-	amph
T. lanatum Benth.	+	-	-	*	-	+	-	-	-	amph
T. lanceolatum Benth.[§]	*	-	-	+	-	+	+	-	-	amph
T. lanceolatum Benth.	+	?	?	+	?	?	+	?	?	amph
T. setaceum Houtt.	+	-	-	*	-	+	-	-	-	amph
Lamieae										
Achyrospermum parviflorum S.Moore	+	-	-	-	-	-	*	+	r	hypo
A. schimperi Perkins	r	-	-	-	-	-	+	*	r	hypo
A. wallichianum Benth. ex Hook.f.	+	+	-	-	-	-	+	*	+	hypo
Acrotome angustifolia G.Taylor	+	-	-	-	-	-	*	+	-	amph
A. fleckii (Gurke) Launert	+	-	-	-	-	-	*	+	-	amph
A. hispida Benth.	+	r	-	-	-	-	*	+	-	amph
A. inflata Benth.	+	-	-	-	-	-	*	+	+	amph

TABLE 1. (*continued*).

Taxa[a]	Stomatal Types[b,c]									Stom. Pos.[d]
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	
Ballota frutescens (L.) J.Woods	*	+	-	-	-	-	r	-	-	amph
B. nigra L. (#1)	+	+	-	-	-	-	*	+	-	hypo
B. nigra L. (#2)	+	+	-	-	-	-	*	+	-	inte
B. pseudodictamnus (L.) Benth.	*	+	-	-	-	-	+	+	-	hypo
Brazoria arenaria Lundell[§]	-	-	-	-	-	-	*	+	-	amph
B. pulcherrima Lundell[§]	-	-	-	-	-	-	*	+	-	amph
B. scutellarioides Engelm. & A.Gray[§]	-	-	-	-	-	-	+	+	*	amph
B. truncata (Benth.) Engelm. & A.Gray[§]	-	-	-	-	-	-	*	+	-	amph
Chamaesphacos ilicifolius Schrenk	*	+	-	-	-	-	*	+	-	amph
Chelonopsis forrestii Anthony[§]	*	+	-	-	-	-	+	-	-	hypo
C. lichiangensis W.Smith	*	?	?	?	?	?	?	?	?	hypo
C. longipes Makino	*	+	-	-	-	-	+	+	-	hypo
C. moschata Miq.	+	?	?	?	?	?	+	?	?	hypo
C. moschata Miq.[§]	*	?	?	?	?	?	+	?	?	hypo
C. odontochila Diels	*	+	-	-	-	-	-	-	-	hypo
Colquhounia coccinea Wallich	*	r	-	-	-	-	r	-	-	hypo
C. seguinii Vaniot	+	+	-	-	-	-	*	+	-	hypo
Craniotome furcata (Link) Kuntze	+	+	-	-	-	-	*	+	+	hypo
C. versicolor Reichb. (#1)	+	?	?	?	?	?	+	+	+	hypo
C. versicolor Reichb. (#2)	+	-	-	-	-	-	+	*	+	hypo
Eremostachys bachardenica B.Fedtsch.	+	+	-	-	-	-	*	+	-	amph
E. iliensis Regel	*	+	-	-	-	-	+	-	-	amph
E. isochila Pazij & Vved.	+	-	-	-	-	-	*	+	-	amph
E. labiosa Bunge	*	+	-	-	-	-	+	-	-	amph
E. regeliana Aitch. & Hemsley	*	+	-	-	-	-	*	+	-	amph
E. speciosa Rupr.	*	-	-	-	-	-	+	-	-	amph
E. tuberosa (Pallas) Bunge	*	+	-	-	-	+	+	-	-	amph
Eriophyton wallichianum Benth.	*	+	-	-	-	-	r	-	-	amph
Galeobdolon luteum Hudson[§]	+	-	-	-	-	-	+	*	+	hypo
Galeopsis ladanum L.	*	+	-	-	-	-	-	-	-	amph
G. ochroleuca Lam.	*	-	-	r	-	-	+	-	-	amph
G. pubescens Besser	*	+	-	-	-	-	+	-	-	hypo
G. tetrahit L.	*	+	-	-	-	-	+	-	-	hypo
Gomphostemma chinense Oliver	+	+	?	?	?	?	+	+	?	hypo
G. crinitum Wallich	+	?	?	?	?	?	*	+	?	hypo
G. lucidum Wallich	+	-	-	-	-	-	*	*	+	hypo
G. velutinum Benth.	+	-	-	-	-	-	*	+	-	hypo
Lagochilus cabulicus Benth.	*	-	-	-	-	-	*	+	-	amph
L. ilicifolius Bunge	+	-	-	-	-	-	*	+	r	amph
L. platycalyx Fischer & C.Meyer (#1)	+	+	-	-	-	-	*	+	-	amph
L. platycalyx Fischer & C.Meyer (#2)	*	-	-	-	-	-	*	+	-	amph
Lagopsis supina (Stephan) Ikonn.-Gal.	*	+	-	-	-	-	+	-	-	amph
Lamiophlomis rotata (Benth.) Kudo	*	+	-	-	-	-	*	+	-	amph
Lamium album L.	+	+	-	-	-	-	*	+	-	inte
L. maculatum L. (#1)	+	+	-	-	-	-	*	+	-	hypo
L. maculatum L. (#2)	+	-	-	-	-	-	+	*	+	hypo
L. moschatum Miller	+	+	-	-	-	-	*	+	-	amph
L. pictum Boiss. & Heldr.	+	+	-	-	-	-	*	+	-	amph
L. purpureum L.[§]	+	+	-	-	-	-	*	+	-	amph

TABLE 1. *(continued).*

Taxa[a]	Stomatal Types[b,c]									Stom. Pos.[d]
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	
Leonotis latifolia Gurke	*	+	-	-	-	-	+	-	-	inte
L. leonitis R.Br.	+	+	-	-	-	-	*	r	-	amph
L. leonurus (L.) R.Br. (#1)	+	?	?	?	?	+	+	?	?	amph
L. leonurus (L.) R.Br. (#2)	*	+	-	-	-	-	+	-	-	inte
L. nepetaefolia (L.) R.Br.	+	+	-	-	-	-	*	+	-	amph
Leonurus cardiaca L.[§]	*	+	-	-	-	-	+	-	-	hypo
L. heterophyllus Sweet	*	+	-	-	-	-	+	-	-	inte
L. macranthus Maxim.	*	+	-	-	-	-	+	-	-	hypo
Leucas altissima Engl.	+	?	?	?	?	?	*	?	?	amph
L. capensis (Benth.) Engl.	*	+	-	-	-	-	+	+	-	amph
L. ciliata Benth.	+	+	-	-	-	-	*	+	-	hypo
L. decemdentata R.Br.	*	+	-	-	-	-	+	+	-	hypo
L. mildbraedii Perkins	*	+	-	-	-	-	+	-	-	hypo
L. mollissima Wallich	+	+	-	-	-	-	*	+	-	inte
Loxocalyx urticifolius Hemsley	+	+	-	-	-	-	*	r	-	hypo
Macbridea alba Chapman[§]	-	-	-	-	-	-	+	+	*	amph
M. caroliniana (Walter) Blake[§]	-	-	-	-	-	-	+	*	+	amph
Marrubium desertii Noë ex Cosson	*	+	-	-	-	-	+	+	-	amph
M. peregrinum L.	*	+	-	-	-	-	+	-	-	amph
M. vulgare L.	*	+	-	-	-	-	+	+	-	amph
M. vulgare L.[§]	*	r	-	-	-	-	+	-	-	amph
Melittis melissophyllum L.[§]	+	+	-	-	-	r	*	+	-	hypo
Metastachydium sagittatum (Regel) C.Y.Wu & Li	*	+	-	-	-	-	+	-	-	amph
Microtoena insuavis (Hance) Prain ex Briq. (#1)	+	-	-	-	-	-	*	+	-	hypo
M. insuavis (Hance) Prain ex Briq. (#2)	+	-	-	-	-	-	*	+	-	hypo
M. moupinensis Franchet ex Prain	*	+	?	?	?	?	+	?	?	hypo
M. robusta Hemsley	*	+	-	-	-	-	+	-	-	hypo
M. urticifolia Hemsley	*	-	-	-	-	-	+	-	-	hypo
Moluccella laevis L.	+	-	-	-	-	-	*	+	-	amph
M. spinosa L.	+	-	-	-	-	-	*	+	r	amph
Notochaete hamosa Benth.	*	+	-	-	-	-	+	+	-	hypo
Otostegia aucheri Boiss.	+	-	-	-	-	-	*	-	-	amph
O. integrifolia Benth.	*	?	?	?	?	?	+	?	?	inte
O. limbata (Benth.) Benth. ex Hook.f.	+	+	-	-	-	-	*	+	-	amph
O. persica (Burm.f.) Boiss.	*	+	-	-	-	-	+	-	-	amph
Panzeria argyracea Kuprian.	*	+	?	?	?	?	?	?	?	inte
Paraphlomis javanica (Blume) Prain ex Backer & Bakh.f.	r	-	-	-	-	-	*	*	r	hypo
P. rugosa (Benth.) Prain	+	+	-	-	-	-	*	+	-	hypo
Phlomidoschema parviflorum (Benth.) Vved.	+	-	-	-	-	r	*	+	-	amph
Phlomis agraria Bunge	*	+	-	-	-	-	+	-	-	amph
P. bracteosa Royle	*	+	-	-	-	-	+	+	-	amph
P. herba-venti L.	+	+	-	-	-	-	*	+	-	hypo
P. maximoviczii Regel	+	+	-	-	-	-	*	+	-	hypo
P. pratensis Karelin & Kir.	*	+	-	-	-	-	+	-	-	amph
P. setigera Falc. ex Benth.	*	r	-	-	-	-	+	r	-	inte
P. taurica Hartw. ex Bunge	+	-	-	-	-	-	*	+	-	amph
P. tuberosa L.	*	+	-	-	-	-	+	-	-	hypo
P. umbrosa Turcz.	*	+	-	-	-	-	*	+	-	hypo

TABLE 1. *(continued).*

Taxa[a]	Stomatal Types[b,c] ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	Stom. Pos.[d]
Phyllostegia brevidens A.Gray	+	+	-	-	-	-	*	+	-	hypo
P. grandiflora (Gaudich.) Benth. (#1)	r	-	-	-	-	-	*	+	+	hypo
P. grandiflora (Gaudich.) Benth. (#2)	+	-	-	-	-	-	*	*	+	hypo
P. hispida Hillebrand	+	+	-	-	-	-	*	+	-	hypo
Physostegia angustifolia Fern.[§]	-	-	-	-	-	-	+	*	+	amph
P. digitalis Small[§]	-	-	-	-	-	-	-	*	+	amph
P. godfreyi Cantino[§]	-	-	-	-	-	-	+	*	-	amph
P. leptophylla Small[§]	-	-	-	-	-	-	+	*	+	amph
P. longisepala Cantino[§]	-	-	-	-	-	-	-	+	*	amph
P. purpurea (Walter) Blake[§]	-	-	-	-	-	-	+	*	+	amph
P. virginiana (L.) Benth.[§]	-	-	-	-	-	-	+	*	+	amph
Prasium majus L. (#1)	*	+	-	-	-	+	*	+	-	hypo
P. majus L. (#2)	*	+	-	-	-	-	+	+	-	hypo
Roylea calycina (Roxb.) Briq.	*	+	-	-	-	-	+	-	-	hypo
Sideritis ambigua Fenzl	+	-	-	-	-	+	*	+	-	amph
S. hirsuta L.	+	-	-	-	-	-	*	+	-	amph
S. ilicifolia Willd.	+	-	-	-	-	-	*	+	-	amph
S. lagascana Willk.	+	-	-	-	-	-	*	+	-	amph
S. lanata L.	+	+	-	-	-	-	*	+	-	amph
S. montana L.	+	-	-	-	-	-	*	+	-	amph
S. perfoliata L.	+	-	-	-	-	-	*	+	-	amph
S. pullulans Vent.	+	r	-	-	-	-	*	r	-	amph
Stachyopsis oblongata (Schrenk) Popov & Vved.	*	+	-	-	-	-	+	-	-	inte
Stachys acerosa Boiss.	+	-	-	-	-	-	*	+	-	amph
S. annua (L.) L.	+	-	-	-	-	-	*	+	-	amph
S. betonica Benth.	+	-	-	-	-	-	*	+	-	amph
S. betonicaeflora Rupr.	+	-	-	-	-	-	*	+	-	amph
S. coccinea Jacq.	+	-	-	-	-	-	*	+	-	amph
S. glutinosa L.	+	-	-	-	-	r	*	+	-	amph
S. labiosa Bertol.	+	-	-	-	-	-	*	+	-	amph
S. riddellii House[§]	+	-	-	-	-	-	*	+	-	hypo
S. spathulata Burchell ex Benth.	+	?	?	?	?	?	+	?	?	amph
S. spruneri Boiss. ex Benth.	+	-	-	-	-	-	*	+	-	amph
S. tenuifolia Willd.[§]	+	-	-	-	-	-	*	+	-	hypo
Stenogyne diffusa A.Gray (#1)	+	-	-	-	-	-	*	*	+	hypo
S. diffusa A.Gray (#2)	*	+	-	-	-	-	*	+	-	hypo
S. kamehamehae Wawra	+	-	-	-	-	-	*	*	-	hypo
S. purpurea H.Mann	+	-	-	-	-	-	+	*	+	hypo
S. rugosa Benth.	+	+	-	-	-	-	*	+	-	hypo
Synandra hispidula (Michx.) Baillon[§]	+	-	-	-	-	-	*	+	r	amph
Thuspeinanta brahuica (Boiss.) Briq.	+	?	?	?	?	?	+	+	?	amph
T. persica (Boiss.) Briq.	+	r	-	-	-	r	*	r	-	amph
Wiedemannia multifida (L.) Benth.	r	r	-	-	-	-	*	+	-	amph
Pogostemoneae										
Colebrookea oppositifolia Smith (#1)	*	?	?	?	?	?	+	?	?	hypo
C. oppositifolia Smith (#2)	+	?	?	?	?	?	+	?	?	hypo
Comanthosphace stellipila S.Moore	+	+	-	-	-	-	*	+	-	hypo
C. sublanceolata (Miq.) S.Moore (#1)	+	+	-	-	-	-	*	+	-	hypo
C. sublanceolata (Miq.) S.Moore (#2)	+	+	-	-	-	-	*	+	-	hypo
Eusteralis cruciata (Benth.) Panigr.	r	-	-	-	-	-	+	*	-	hypo
E. sampsonii (Hance) Panigr.	+	-	-	-	-	-	*	+	-	amph
E. stellata (Lour.) Panigr. (#1)	-	-	-	-	-	-	+	*	+	amph
E. stellata (Lour.) Panigr. (#2)	-	-	-	-	-	-	+	*	+	amph

TABLE 1. (*continued*).

Taxa[a]	Stomatal Types[b,c]									Stom. Pos.[d]
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	
Pogostemon cablin (Blanco) Benth.	r	-	-	-	-	-	+	*	+	inte
P. elsholtzioides Benth.	r	-	-	-	-	-	*	+	-	hypo
P. glaber Benth. (#1)	+	-	-	-	-	-	+	*	r	hypo
P. glaber Benth. (#2)	+	-	-	-	-	-	+	*	+	inte
P. heyneanus Benth.[§]	-	-	-	-	-	-	+	*	+	hypo
P. plectranthoides Desf.	+	-	-	-	-	-	+	*	+	hypo
Rostrinucula dependens (Rehder) Kudo	+	-	-	-	-	-	*	+	-	hypo
Prostantheroideae										
Hemiandra pungens R.Br.	r	-	-	*	-	r	-	-	-	amph
Hemigenia incana Benth. (#1)	+	-	-	*	-	r	-	-	-	amph
H. purpurea R.Br.	*	-	-	*	-	-	-	-	-	amph
H. saligna Diels	+	-	-	*	-	-	-	-	-	amph
Microcorys brevidens Benth.	*	-	-	+	-	+	-	-	-	amph
M. ericifolia Benth.	*	-	-	+	-	-	-	-	-	amph
Prostanthera aspalathoides Cunn. ex Benth.	*	-	-	*	-	+	-	-	-	amph
P. cuneata Benth.	+	-	-	*	+	+	-	-	-	inte
P. euphrasioides Benth.	+	-	-	*	+	-	-	-	-	amph
P. lasianthos Labill. (#1)	*	-	-	*	r	+	r	-	-	hypo
P. lasianthos Labill. (#2)	+	-	-	*	+	r	r	-	-	hypo
P. nivea Cunn. ex Benth. (#1)	+	-	-	*	+	+	-	-	-	amph
P. nivea Cunn. ex Benth. (#2)	*	-	-	*	+	+	-	-	-	amph
P. ovalifolia R.Br.	*	+	-	+	-	+	-	-	-	hypo
P. rotundifolia R.Br.[§]	*	+	-	+	-	r	+	-	-	amph
P. rotundifolia R.Br.	*	+	-	*	-	+	-	-	-	inte
P. saxicola R.Br.	+	+	-	*	+	+	-	-	-	amph
Westringia amabilis J.Boivin	*	r	-	+	r	-	-	-	-	hypo
W. brevifolia Benth.	*	*	-	r	-	-	-	-	-	hypo
W. cheelii Maiden & Betche	*	+	-	-	-	-	-	-	-	amph
W. fruticosa (Willd.) Druce	*	+	-	r	-	+	-	-	-	hypo
Scutellarieae										
Salazaria mexicana Torrey (#1)	*	+	-	-	-	-	*	+	-	amph
S. mexicana Torrey (#2)	+	+	-	-	-	-	*	+	-	amph
Scutellaria amoena C.H.Wright	+	-	-	-	-	-	*	+	+	amph
S. elliptica Muhlenb.[§]	+	-	-	-	-	-	+	*	+	hypo
S. gardoquioides Benth.	*	-	-	-	-	-	+	-	-	hypo
S. hirtella Juz.	?	?	?	?	?	?	*	+	?	inte
S. incana Biehler[§]	+	+	-	-	-	-	*	+	r	hypo
S. integrifolia L.[§]	+	-	-	-	-	-	*	*	r	inte
S. lateriflora L.[§]	+	+	-	-	-	-	*	+	-	hypo
S. multicaulis Boiss.	+	+	-	-	-	-	*	+	-	amph
S. nervosa Pursh[§]	+	-	-	-	-	-	*	+	-	hypo
S. orientalis L.	+	-	-	-	-	-	*	+	-	inte
S. ovata Hill[§]	+	-	-	-	-	-	*	*	+	hypo
S. serrata Andrz.[§]	+	-	-	-	-	-	*	+	-	hypo
Uncertain Tribal Affin.										
Ajugoides humilis (Miq.) Makino (#1)	+	+	-	-	-	-	*	+	-	hypo
A. humilis (Miq.) Makino (#2)	*	+	-	-	-	-	*	+	-	hypo
Anisomeles heyneana Benth.	+	-	-	-	-	-	*	+	-	hypo
A. indica (L.) Kuntze (#1)	+	?	?	?	?	?	*	+	?	amph
A. indica (L.) Kuntze (#2)	+	?	?	?	?	?	*	+	?	amph
A. malabarica (L.) R.Br. ex Sims (#1)	+	-	-	-	-	-	*	+	-	hypo
Eurysolen gracilis Prain (#1)	+	-	-	-	-	-	*	+	+	hypo
E. gracilis Prain (#2)	+	+	-	-	-	-	*	+	-	hypo
Hypogomphia turkestana Bunge	+	-	-	-	-	-	*	+	-	amph
Suzukia shikikunensis Kudo	+	+	-	-	-	-	*	+	-	hypo

TABLE 1. (*continued*).

Taxa[a]	Stomatal Types[b,c]									Stom. Pos.[d]
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	
Nepetoideae										
"Mentheae"										
Ceratominthe odora (Griseb.) Hauman	+	+	-	-	-	-	*	-	-	hypo
Collinsonia canadensis L. (#1)	+	+	-	-	-	-	*	+	-	hypo
C. canadensis L. (#2)	+	+	-	-	-	-	*	+	-	hypo
Cunila origanoides (L.) Britt.	+	-	-	-	-	-	*	+	-	inte
Cyclotrichium origanifolium (Labill.) Manden. & Scheng.	+	-	-	-	-	-	*	+	-	amph
Elsholtzia patrinii (Lepechin) Garcke	+	+	-	-	-	-	*	+	-	inte
Hedeoma drummondii Benth.	-	-	-	-	-	-	+	*	+	amph
H. graveolens Chapman ex A.Gray	+	-	-	-	-	-	*	+	-	amph
H. nanum (Torrey) Briq.	+	-	-	-	-	-	*	+	-	amph
Keiskea japonica Miq.	+	-	-	-	-	-	*	+	-	hypo
Lepechinia hastata (A.Gray) Epling	+	-	-	-	-	-	*	+	-	amph
Lycopus americanus Muhlenb.	+	-	-	-	-	-	*	+	-	inte
L. rubellus Moench	+	+	-	-	-	-	*	+	-	amph
L. virginicus L.	r	-	-	-	-	-	+	*	+	hypo
Melissa officinalis L. (#1)	+	-	-	-	-	-	*	+	-	hypo
M. officinalis L. (#2)	+	+	-	-	-	-	*	+	-	hypo
Mentha arvensis L.	r	-	-	-	-	-	*	*	-	hypo
M. citrata Ehrh.	r	-	-	-	-	-	*	+	+	hypo
M. piperita L.	r	-	-	-	-	-	*	+	-	hypo
Micromeria biflora Benth.	+	-	-	-	-	-	*	+	-	hypo
M. punctata Benth.	+	-	-	-	-	-	*	+	-	hypo
Monardella odoratissima Benth.	+	-	-	-	-	-	*	*	-	amph
M. villosa Benth.	+	-	-	-	-	-	*	+	r	amph
Perillula reptans Maxim. (#1)	+	-	-	-	-	-	+	*	r	hypo
P. reptans Maxim. (#2)	+	+	-	-	-	-	*	+	r	hypo
Pogogyne zizyphoroides Benth.	+	-	-	-	-	-	+	*	-	amph
Poliomintha glabrescens A.Gray ex Hemsl.	+	-	-	-	-	-	*	+	r	amph
Pycnanthemum albescens A.Gray	+	?	?	?	?	?	+	+	+	hypo
P. floridanum E.Grant & Epling	-	-	-	-	-	-	+	*	-	hypo
P. aff. incanum (L.) Michaux	+	-	-	-	-	-	+	*	-	hypo
Rhabdocaulon strictum (Benth.) Epling	-	-	-	-	-	-	+	*	-	hypo
Rhododon ciliatus (Benth.) Epling	r	-	-	-	-	-	*	+	-	amph
Satureja arkansana (Nutt.) Briq.	+	-	-	-	-	-	*	+	-	amph
S. douglasii (Benth.) Briq.	+	-	-	-	-	-	*	+	-	hypo
S. parvifolia (Philippi) Epling	+	+	-	-	-	-	*	+	-	hypo
S. popovii B.Fedtsch. & Gontch.	r	-	-	-	-	-	*	+	-	amph
S. vulgaris (L.) Fritsch	+	-	-	-	-	-	*	+	r	hypo
Thymus serpyllum L.	+	-	-	-	-	-	*	+	-	inte
Nepeteae										
Agastache breviflora (A.Gray) Epling	-	-	-	-	-	-	+	*	+	amph
A. cana (Hook.) Wooton & Standley	+	r	-	-	-	+	*	+	-	amph
A. nepetoides (L.) Kuntze	+	-	-	-	-	r	*	+	r	hypo
A. pallidiflora (A.A.Heller) Rydb.	+	-	-	-	-	-	*	+	-	amph
A. scrophulariaefolia (Willd.) Kuntze	+	+	-	-	-	-	*	*	+	hypo

TABLE 1. (*continued*).

Taxa[a]	Stomatal Types[b,c]									Stom. Pos.[d]
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	
Cedronella canariensis (L.) Webb & Berth. (#1)	+	+	-	-	-	-	*	+	-	hypo
C. canariensis (L.) Webb & Berth. (#2)	+	+	-	-	-	-	*	+	r	hypo
Dracocephalum hemsleyanum (Prain) Marquand	+	?	?	?	?	?	+	?	?	inte
D. heterophyllum Benth.	r	r	-	-	-	-	*	+	+	amph
D. parviflorum Nutt.	+	-	-	-	-	-	*	+	-	amph
D. ruyschiana L.	+	+	-	-	-	+	*	+	-	inte
Glechoma hederacea L.	+	-	-	-	-	-	*	*	+	hypo
Lophanthus chinensis Benth.	+	-	-	-	-	-	*	+	-	amph
Meehania cordata (Nutt.) Britton	-	-	-	-	-	-	+	*	r	hypo
Nepeta cataria L.	+	-	-	-	-	-	*	+	-	amph
N. clarkei Hook.f.	+	-	-	-	-	-	*	+	-	amph
N. curviflora Boiss.	+	?	?	?	?	?	*	?	?	amph
N. discolor Royle ex Benth.	+	-	-	-	-	-	*	+	-	amph
N. nepetella L.	+	-	-	-	-	-	*	+	-	amph
Prunella vulgaris L.	-	-	-	-	-	-	r	*	+	inte
Ocimeae										
Acrocephalus fruticosus Dunn	+	-	-	-	-	-	*	+	-	amph
A. indicus Kuntze	+	-	-	-	-	-	*	+	-	inte
Asterohyptis stellulata (Benth.) Epling	+	+	-	-	-	-	*	+	-	inte
Catopheria capitata Benth. ex Hemsley (#1)	r	-	-	-	-	-	*	+	r	hypo
C. capitata Benth. ex Hemsley (#2)	?	?	?	?	?	?	+	*	?	hypo
Eriope crassipes Benth.	+	-	-	-	-	-	*	+	-	amph
Eriopidion strictum (Benth.) R.Harley	r	-	-	-	-	-	*	+	-	amph
Fuerstia africana T.C.E.Fries	+	?	?	?	?	?	+	?	?	hypo
Haumaniastrum coeruleum (Oliver) Duvign. & Plancke	-	-	-	-	-	-	+	*	+	amph
Hemizygia canescens (Gurke) Ashby	-	-	-	-	-	-	+	*	+	amph
Holostylon strictipes G.Taylor	+	-	-	-	-	-	*	+	-	amph
Hyptis alata (Raf.) Shinn.	+	-	-	-	-	-	*	r	-	amph
H. emoryi Torrey	*	-	-	-	-	-	+	+	-	amph
H. mutabilis (Rich.) Briq.	+	-	-	-	-	-	*	+	-	inte
H. oblongifolia Benth.	+	-	-	-	-	-	*	+	-	hypo
Icomum lineare Burkill	-	-	-	-	-	-	*	+	-	amph
Lavandula multifida L.	*[e]	-	-	-	-	-	+	+	-	amph
L. stoechas L.	+	-	-	-	-	-	*	+	-	amph
Nautochilus labiatus (N.E.Br.) Bremek.	+	+	-	-	-	-	*	+	-	hypo
Ocimum americanum L.	+	-	-	-	-	-	*	+	-	amph
O. basilicum L.	+	-	-	-	-	-	*	+	-	amph
O. gratissimum L. (#1)	+	-	-	-	-	-	*	+	-	inte
O. gratissimum L. (#2)	+	-	-	-	-	-	*	*	+	inte
Orthosiphon affinis N.E.Br.	+	-	-	-	-	-	*	+	-	amph
O. aristatus (Blume) Miq.	+	-	-	-	-	-	+	*	+	hypo
O. spiralis (Lour.) Merr.	+	-	-	-	-	-	*	+	-	inte
Plectranthastrum clerodendroides T.C.E Fries	-	-	-	-	-	-	+	*	+	hypo

TABLE 1. (*continued*).

Taxa[a]	Stomatal Types[b,c] ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	Stom. Pos.[d]
Plectranthus forsteri Benth.	r	-	-	-	-	-	*	*	r	amph
P. scutellarioides (L.) R.Br.	+	-	-	-	-	-	*	+	-	hypo
Rabdosia excisa (Maxim.) H.Hara	+	+	-	-	-	-	*	r	-	hypo
R. inflexa (Thunb.) H.Hara	*	+	-	-	-	-	*	+	-	hypo
R. nervosa (Hemsley) C.Y.Wu & Li	*	+	-	-	-	-	*	+	-	inte
Solenostemon scutellarioides L.Codd (#1)	+	-	-	-	-	-	*	*	-	amph
Syncolostemon densiflorus Benth.	+	-	-	-	-	-	*	+	-	amph
"Salvieae"										
Arischrada bucharica (Popov) Pobed.	r	-	-	-	-	-	+	*	+	amph
Blephilia hirsuta (Pursh) Benth.[§]	+	r	-	-	-	-	*	+	-	hypo
Monarda clinopodia L.	+	-	-	-	-	-	*	+	-	hypo
M. fistulosa L.[§]	?	?	?	?	?	?	?	*	?	hypo
M. punctata L.	+	-	-	-	-	-	*	+	-	amph
Perovskia abrotanoides Karelin	+	+	-	-	-	-	*	+	-	amph
P. atriplicifolia Benth.	+	+	-	-	-	-	*	+	-	amph
Salvia carnosa Douglas	+	?	?	?	?	?	+	?	?	amph
S. farinacea Benth.	+	-	-	-	-	-	*	+	-	amph
S. lyrata L.	-	-	-	-	-	-	*	*	r	amph
S. reflexa Hornem.	+	-	-	-	-	-	*	*	-	amph
Verbenaceae										
Avicennioideae										
Avicennia nitida Jacq.	+	-	-	-	-	-	*	-	-	hypo
Caryopteridoideae										
Caryopterideae										
Caryopteris grata Benth.	*	+	-	-	-	-	+	-	-	hypo
C. incana (Thunb.) Miq. (#1)	+	+	?	?	?	?	?	?	?	hypo
C. mongholica Bunge (#1)	*	+	-	+	-	-	-	-	-	amph
C. mongholica Bunge (#2)	*	+	-	+	-	-	-	-	-	amph
C. nepetaefolia (Benth.) Maxim.	*	+	-	-	-	r	+	-	-	hypo
C. odorata (Ham.) Robinson	+	+	-	-	-	-	*	+	-	hypo
C. terniflora Maxim.	+	r	-	-	-	-	*	+	-	hypo
Glossocarya siamensis Craib	*	+	-	+	-	-	-	-	-	hypo
Petraeovitex kinabaluensis Munir	+	-	-	-	-	+	*	+	-	hypo
P. multiflora (Smith) Merr.	*	+	-	-	-	+	+	-	-	hypo
Teijsmanniodendreae										
Teijsmanniodendron ahernianum (Merr.) Bakh.	*	+	-	-	-	-	-	-	-	hypo
T. subspicatum (H.Hallier) Kosterm.	*	+	-	-	-	+	r	-	-	hypo
Chloanthoideae										
Achariteae										
Nesogenes dupontii Hemsley	*	-	-	-	-	-	r	-	-	amph
N. euphrasioides (Hook. & Arn.) A.DC.	*	-	-	-	-	-	-	-	-	amph
Spartothamnella puberula (F.Muell.) Maiden & Betche (#1)	*	-	-	+	-	+	-	-	-	hypo
S. puberula (F.Muell.) Maiden & Betche (#2)	*	+	-	+	-	+	r	-	-	hypo
S. puberula (F.Muell.) Maiden & Betche (#3)	*	+	-	+	-	-	-	-	-	inte
Chloantheae										
Chloanthes stoechadis R.Br.	+	-	-	*	-	-	-	-	-	hypo
Cyanostegia angustifolia Turcz.	*	-	-	+	-	+	-	-	-	amph
C. microphylla S.Moore	+	-	-	*	+	-	-	-	-	amph

TABLE 1. *(continued)*.

Taxa[a]	Stomatal Types[b,c] ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	Stom. Pos.[d]
Physopsideae										
Dicrastylis exsuccosa (F.Muell.) Druce	*	-	-	+	-	-	-	-	-	amph
Newcastelia cephalantha F.Muell.	r	-	-	*	+	-	-	-	-	amph
Nyctanthoideae										
Nyctanthes arbor-tristis L.	*	+	-	-	-	-	-	-	-	hypo
Phrymoideae										
Phryma leptostachya L.	*	+	-	r	-	-	r	-	-	hypo
Symphorematoideae										
Congea chinensis Mold.	+	+	-	*	-	+	-	-	-	hypo
C. forbesii King & Gamble	*	+	-	+	-	+	-	-	-	hypo
C. tomentosa Roxb.	*	+	?	+	?	?	?	?	?	hypo
Sphenodesme ferruginea (Griffith) Briq.	+	?	?	?	?	*	?	?	?	hypo
S. pentandra Jack	*	-	-	-	-	+	-	-	-	hypo
Symphorema luzonicum (Blanco) Fernandez-Villar	+	+	-	-	-	*	-	-	-	hypo
Verbenoideae										
Citharexyleae										
Citharexylum affine D.Don	*	+	-	-	-	-	-	-	-	inte
C. berlandieri Robinson	*	+	-	+	-	-	-	-	-	hypo
C. caudatum L.	*	r	-	+	-	-	-	-	-	hypo
C. ligustrinum Van Houtte	*	+	-	-	-	-	-	-	-	hypo
C. punctatum Greenman	+	*	-	-	-	-	-	-	-	hypo
Duranta mandonii Mold.	*	-	+	-	-	+	-	-	-	hypo
D. mutisii L.f.	*	+	+	-	-	+	-	-	-	hypo
D. peruviana Mold.	*	-	+	-	-	+	-	-	-	hypo
D. repens L. (#1)	*	-	-	+	+	+	-	-	-	hypo
Rehdera trinervis (S.F.Blake) Mold.	*	+	-	-	-	-	-	-	-	hypo
Rhaphithamnus spinosus (A.L.Juss.) Mold.	*	+	-	-	-	-	-	-	-	hypo
Lantaneae										
Aloysia gratissima (Gill. & Hook.) Tronc.	*	?	?	?	?	?	?	?	?	amph
Bouchea fluminensis (Vell.Conc.) Mold.	+	-	-	-	-	-	*	+	-	hypo
B. prismatica (L.) Kuntze	*	+	-	-	-	-	*	+	-	amph
Diostea juncea (Gillies & Hook.) Miers	*	*	-	-	-	-	-	-	-	amph
Lantana horrida Kunth (#1)	*	+	-	r	-	r	*	-	-	amph
L. horrida Kunth (#2)	*	+	-	+	-	r	+	r	-	amph
L. involucrata L.	*	-	-	+	-	+	+	-	-	inte
Lippia graveolens Kunth	*	r	-	-	-	-	+	-	-	hypo
Phyla incisa Small	+[e]	-	-	-	-	+	*	+	-	amph
P. lanceolata (Michaux) E.Greene[§]	+[e]	-	-	-	-	r	*	*	r	amph
P. nodiflora (L.) E.Greene	+[e]	-	-	-	-	*	*	+	-	amph
Priva aspera Kunth	*	+	-	-	-	r	+	-	-	amph
P. grandiflora (Ortega) Mold.	*	+	?	?	?	?	?	?	?	amph
Stachytarpheta frantzii Polak.	+	+	-	-	-	-	*	r	-	inte
S. jamaicensis (L.) Vahl	+	+	-	-	-	-	*	r	-	amph
Monochileae										
Amasonia campestris (Aublet) Mold.	*	+	-	-	-	-	*	+	-	hypo
A. hirta Benth.	+	+	-	-	-	-	*	+	-	amph

TABLE 1. (*continued*).

Taxa[a]	Stomatal Types[b,c]									Stom. Pos.[d]
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	
Petreeae										
Casselia hymenocalyx Briq.	+	-	-	-	-	-	*	r	-	hypo
Petrea amazonica Mold.	+	-	-	-	-	-	+	*	+	hypo
P. arborea Kunth	+	?	?	?	?	?	+	?	?	hypo
P. volubilis L. (#1)	+	-	-	-	-	-	*	-	-	hypo
P. volubilis L. (#2)	+	+	-	-	-	+	*	-	-	hypo
Verbeneae										
Glandularia bipinnatifida (Nutt.) Nutt.	*	-	-	-	-	-	+	-	-	amph
G. canadensis (L.) Small	*	+	-	-	-	-	-	-	-	amph
Hierobotana inflata (Kunth.) Briq.	+	?	?	?	?	?	?	?	?	hypo
Junellia ligustrina (Lagascana) Mold.	*	+	-	-	-	-	-	-	-	amph
Tamonea curassavica (L.) Pers.	+	?	?	?	?	?	*	?	?	amph
Verbena hastata L.[§]	*	r	-	-	-	-	+	-	-	hypo
V. litoralis Kunth	*	+	-	+	-	r	r	-	-	amph
V. macdougalii A.A.Heller	*	+	-	+	-	-	r	-	-	amph
V. pumila Rydb.	*	+	-	-	-	-	+	-	-	amph
V. urticifolia L.[§]	*	+	-	-	-	-	-	-	-	hypo
Viticoideae										
Callicarpeae										
Aegiphila aculeifera Mold.	+	*	-	-	-	-	-	-	-	hypo
A. deppeana Steudel	+	+	-	*	+	-	-	-	-	hypo
A. pendula Mold.	*	+	-	+	-	-	+	-	-	hypo
Callicarpa americana L.	*	+	-	-	-	-	+	-	-	hypo
C. dichotoma (Lour.) K.Koch	*	+	?	?	?	?	?	?	?	hypo
C. mollis Siebold & Zucc.	*	+	-	-	-	-	+	-	-	hypo
Clerodendreae										
Clerodendrum aculeatum (L.) Schldl.	*	+	-	-	-	-	-	-	-	hypo
C. anafense Britton & P.Wilson	*	+	-	+	-	+	-	-	-	hypo
C. capitatum (Willd.) Schum. & Thonn.	*	+	-	-	-	-	-	-	-	hypo
C. cuneatum Gurke	+	+	-	-	-	r	*	+	r	amph
C. floribundum R.Br.	*	+	-	r	-	+	-	-	-	amph
C. glabrum E.Meyer	*	+	-	-	-	-	-	-	-	inte
C. inerme (L.) Gaertner	*	*	-	r	-	-	-	-	-	hypo
C. myricoides (Hochst.) R.Br.	*	+	-	-	-	-	*	+	-	hypo
C. philippinum Schauer	*	+	-	+	-	-	-	-	-	hypo
C. squiresii Merr.	*	+	-	-	-	+	-	-	-	hypo
C. trichotomum Thunb.	*	+	-	-	-	-	-	-	-	hypo
Faradaya amicorum (Seemann) Seemann	*	+	-	-	-	-	-	-	-	hypo
F. ovalifolia (A.Gray) Seemann	*	-	-	+	-	-	-	-	-	hypo
F. splendida F.Muell.	*	+	-	-	-	-	-	-	-	hypo
Holmskioldia sanguinea Retz. (#1)	*	+	-	+	-	-	-	-	-	hypo
H. sanguinea Retz. (#2)	*	+	-	+	-	r	+	-	-	hypo
H. sanguinea Retz. (#3)	*	+	-	+	-	-	r	-	-	hypo
H. tettensis (Klotzsch) Vatke	+	*	-	r	-	-	-	-	-	hypo
Kalaharia spinescens Gurke	*	-	-	+	-	+	-	-	-	amph
Karomia fragrans Dop	*	+	-	+	-	+	r	-	-	hypo
Oxera morierii Vieill.	+	-	-	*	+	+	-	-	-	hypo
O. neriifolia Beauv.	+	+	-	*	+	+	-	-	-	hypo
O. sulfurea Dubard	+	+	-	*	+	+	-	-	-	hypo
Teucridium parvifolium Hook.f.	*	+	-	+	-	-	+	-	-	hypo

TABLE 1. *(continued)*.

Taxa[a]	Stomatal Types[b,c] ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	Stom. Pos.[d]
Viticeae										
Cornutia grandiflora (Cham. & Schldl.) Schauer	*	+	-	-	-	-	+	-	-	hypo
C. pyramidata L.	*	?	?	?	?	?	+	?	?	hypo
Garrettia siamensis Fletcher	+	?	?	?	?	?	?	?	?	hypo
Gmelina delavayana Dop	*	+	-	-	-	-	-	-	-	hypo
G. moluccana (Blume) Backer	*	+	-	-	-	+	-	-	-	hypo
G. racemosa (Lour.) Merr.	*	+	?	?	?	?	?	?	?	hypo
Premna barbata Wallich	+	-	-	-	-	-	*	+	-	hypo
P. corymbosa Willd.	+	-	-	-	-	-	*	*	+	hypo
P. foetida Reinw.	+	-	-	-	-	-	*	+	-	hypo
P. japonica Miq.	*	+	-	-	-	-	+	-	-	hypo
P. octonervia Merr. & Metcalf	*	+	-	-	-	-	*	-	-	hypo
Pseudocarpidium avicennioides (A.Rich.) Millsp.	*	+	-	-	-	-	-	-	-	hypo
P. wrightii Millsp.	*	+	-	-	-	-	-	-	-	hypo
Tsoongia axillariflora Merr.	+	-	-	*	-	+	-	-	-	hypo
Vitex agnus-castus L.	*	+	-	-	-	-	-	-	-	hypo
V. cannabifolia Siebold & Zucc.	*	+	-	+	-	r	-	-	-	hypo

[a]If name is followed by the symbol §, data are from Abu-Asab and Cantino (1987a). All other data are from the present survey. #1, #2, etc. refer to different specimens of a species; the numbers correspond to entries in the voucher list deposited in four major botanical libraries (see Materials and Methods).

[b]Stomatal Types: ANO, anomocytic; ACT, actinocytic; CYC, cyclocytic; ANI, anisocytic; HEL, helicocytic; PAR, paracytic; DI2, diacytic (2 subsidiary cells); DI3, 3-celled diallelocytic; DI4, 4-celled diallelocytic.

[c]Symbols: *, commonest type(s); +, present; r, rare (no more than two examples found); -, absent; ?, unknown whether present or absent (stomata are poorly stained or obscured by dense trichomes).

[d]Stomatal Position: amphistomatic, hypostomatic, or intermediate (i.e., a few stomata on the adaxial surface).

[e]Rare stomatal types: staurocytic, in Lavandula multifida; parallelocytic, in the three species of Phyla.

istic of the Labiatae. The fundamental structure of the nonglandular trichomes (i.e., unicellular vs. multicellular and simple vs. branched) was also noted. The classification system developed by Abu-Asab and Cantino (1987a) for the subsessile glandular trichomes in subtribe Melittidinae was found to apply well to the Labiatae as a whole and is used here (see the APPENDIX). For it to extend to the Verbenaceae, an additional gland type (type 11) was added.

RESULTS

TABLES 1 and 2 require some introductory comments. Because the leaves of some species stained poorly, and the subsessile glands and stomata in others were obscured by a dense layer of nonglandular trichomes, the tables are heavily laden with question marks. Even when the data are incomplete, however, some information may be inferred. For example, type 5 glands were definitely present

on the leaves of *Tinnea apiculata* (see TABLE 2, under "Ajugeae"), and more complex glands were present as well, but it was unclear whether they were type 8, 9, or 10. On the other hand, types 1–4, 6, 7, and 11 were definitely absent.

A species has been included in a table only if there were clear observations to tabulate with regard to the characters of concern. Each table therefore includes some species not found in the other. For example, *Acrotome angustifolia* is present in TABLE 1 but not TABLE 2 because the stomatal complexes stained sufficiently for their configurations to be discerned but the subsessile glands did not stain well enough to be classified as to type.

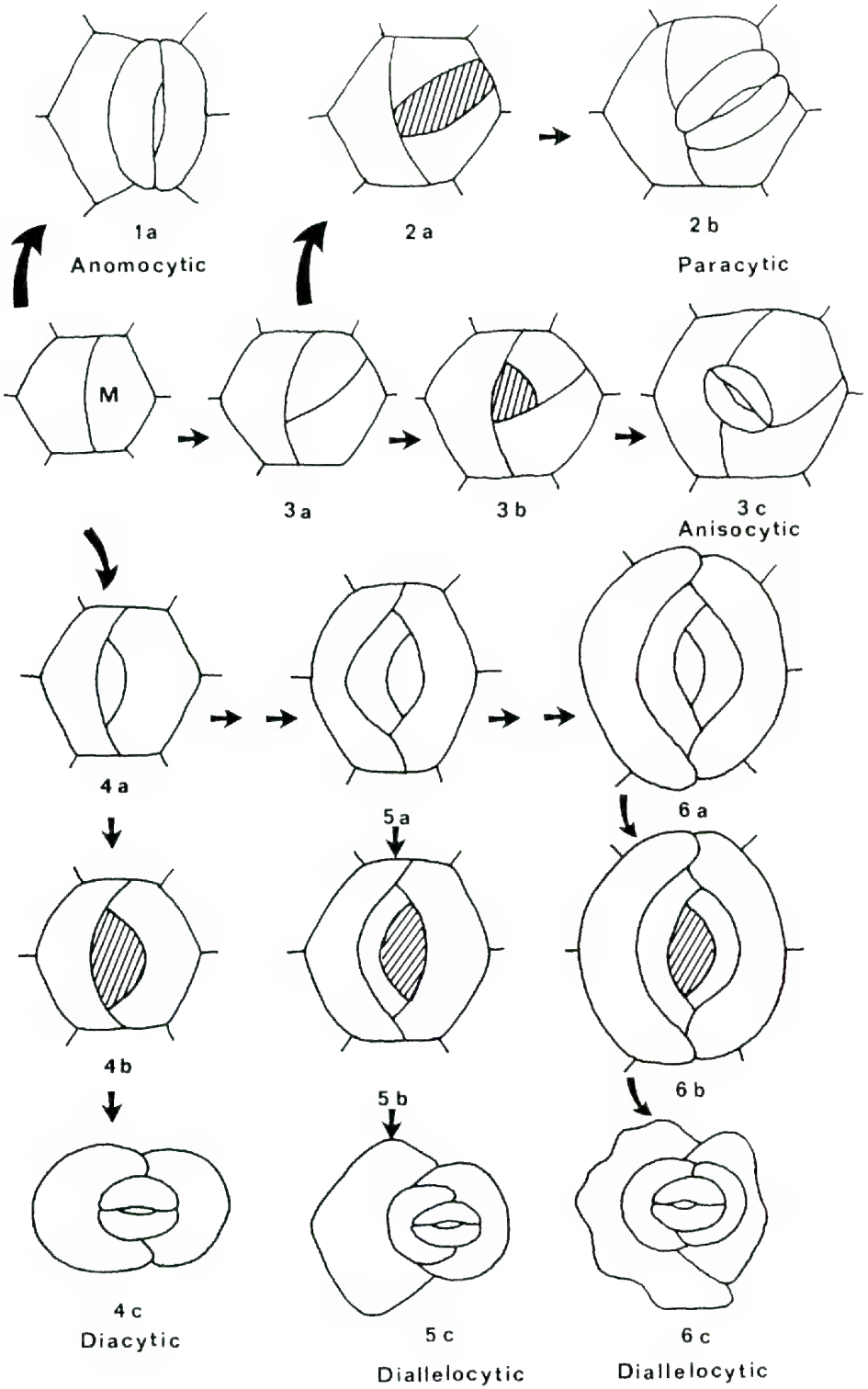
For subsessile glands and stomatal complexes I have indicated relative abundance by designating with an asterisk the most common gland and stomatal types in a species. If no asterisk is present, it may be because subsessile glands were so infrequent that a meaningful estimate of relative abundance could not be made or, alternatively, because such a high proportion of the glands (or stomata) were poorly stained or hidden by nonglandular trichomes that relative abundance could not be estimated. If two or more types of stomata or glands are marked with an asterisk, they were roughly equal in abundance on the leaf surface (or, occasionally, one type was most abundant on the abaxial surface and another on the adaxial).

In order to provide a more comprehensive survey and facilitate comparison of taxa, data published by Abu-Asab and Cantino (1987a) are included in the tables. Because actinocytic stomata were not distinguished from anomocytic in the earlier study (discussed below), the slides used by Abu-Asab and Cantino were reexamined to determine the distribution of actinocytic stomata. In the process, a few other errors of omission were discovered. When discrepancies exist between the earlier paper and this one, the data here should be assumed to be correct.

In TABLES 1 and 2 the names of a few suprageneric taxa of Labiatae (Lamioideae, Ajugeae, Mentheae, Salvieae) are placed in quotation marks to indicate that these taxa are probably not monophyletic (see Taxonomic Background). No attempt was made to do the same for the Verbenaceae, in which phylogenetic relationships are less well understood.

STOMATA

Ten types of stomatal complexes were observed (definitions adapted from Payne, 1970, Dilcher, 1974, and Wilkinson, 1979): actinocytic (stoma surrounded by a single ring of five or more radially elongate cells enclosing the guard cells); anisocytic (stoma surrounded by three subsidiary cells, one of which is markedly smaller than the other two); anomocytic (stoma surrounded by cells that are indistinguishable from other epidermal cells); cyclocytic (stoma surrounded by a single ring of small subsidiary cells); diacytic (stoma enclosed by a pair of subsidiary cells whose common walls are perpendicular to the guard cells); diallelocytic (stoma enclosed by an alternating complex of three or more C-shaped subsidiary cells of graded sizes oriented perpendicular to the guard cells); helicocytic (stoma surrounded by a helix of four or more cells); paracytic (stoma bordered on either side by one or more subsidiary cells whose


1a
Anomocytic
2a
2b
Paracytic
M
3a
3b
3c
Anisocytic
4a
5a
6a
4b
5b
6b
4c
Diacytic
5c
Diallelocytic
6c
Diallelocytic

long axes parallel those of the guard cells; subsidiary cells may or may not meet over the poles); parallelocytic (stoma with an alternating complex of three or more C-shaped subsidiary cells of graded sizes oriented parallel to the guard cells); staurocytic (stoma surrounded by three or four similar subsidiary cells with anticlinal walls arranged crosswise to the guard cells).

The actinocytic type, scored as anomocytic by Abu-Asab and Cantino (1987a), is recognized here with reservations. The term has been used differently by different authors (discussed by Baranova, 1987) and is considered by Stace (1965) to be a mere modification of the anomocytic type. As a rule of thumb, I have scored a stomatal complex as actinocytic if there are at least five radially elongate subsidiary cells that are longer than the other epidermal cells. Using this definition, however, many stomatal complexes were scored as actinocytic that closely resemble what Wilkinson (1979, *fig. 10.3a*) considered to be anomocytic. Others scored here as actinocytic might be classified by some workers as stephanocytic, a newly described stomatal complex (Baranova, 1987) that is intermediate between the actinocytic and cyclocytic types. Wilkinson (1979, p. 99) noted that "giant or hydathodic stomata" are frequently actinocytic. Those observed in the present study were frequently, but not invariably, larger than the other stomata on the leaf.

As discussed by Abu-Asab and Cantino (1987a), two kinds of diallelocytic stomata occur in the Labiatae, one with three subsidiary cells and the other with four. Because they do not always occur together (the latter is much rarer than the former), they have been listed separately in TABLE 1.

Stomatal ontogeny was not systematically studied, but ontogenies could sometimes be inferred from the morphology of mature stomatal complexes. The ontogenetic pathways of most stomatal types that are common in the Labiatae and Verbenaceae are shown in FIGURE 1.

Anomocytic and diacytic stomata were the most frequently encountered types in both the Labiatae and the Verbenaceae (see TABLE 1). The former were observed in all Verbenaceae and the vast majority of Labiatae examined, the latter in slightly more than half the genera of Verbenaceae and all genera of Labiatae except in tribe Prostanthereae, where they were rare.

Diallelocytic stomata are far more frequent in the Labiatae than in the Verbenaceae. In the Labiatae diallelocytic stomata with three subsidiary cells were found in nearly all species of subfam. Nepetoideae and tribes Pogostemoneae and Scutellarieae, in most genera of Lamieae, and in six genera of Ajugeae, but they have not been found in tribe Prostanthereae. In the Verbenaceae three-celled diallelocytic stomata were found in all examined species of *Amasonia* L. f., *Bouchea* Cham., *Phyla* Lour., *Stachytarpheta* M. Vahl, and *Clerodendrum* L. subg. *Cyclonema* (Hochst.) Gurke, three species of *Premna*

FIGURE 1. Stomatal ontogenetic pathways: anomocytic (1a), paracytic (2a, b), anisocytic (3a–c), diacytic (4a–c), diallelocytic with 3 subsidiary cells (5a–c), diallelocytic with 4 subsidiary cells (6a–c). (M = meristemoid, *sensu* Fryns-Claessens & Van Cotthem, 1973.) (Ontogenies of diacytic and 4-celled diallelocytic stomata adopted from Payne, 1970. Figure originally published in Abu-Asab & Cantino, 1987a.)

L., two species of *Caryopteris* Bunge, and four other scattered species. Diallelocytic stomata with four subsidiary cells are very rare in the Verbenaceae. In the Labiatae they are widespread, occurring in every tribe except the Prostanthereae, but their distribution within genera is very inconstant: although observed in 44 genera of the family, in only four were they found in all examined species (excluding those in which only one species was studied).

Anisocytic stomata are widespread in the Verbenaceae and particularly common in the Chloanthoideae and the Clerodendreae. In the Labiatae they are essentially restricted to the two tribes that lack a gynobasic style—the Ajugeae and the Prostanthereae. Particularly characteristic of the Prostanthereae, anisocytic stomata were found in nearly every species and were the most common type in three of the five genera examined. In the Ajugeae they were found in all examined specimens of *Tetraclea* A. Gray and *Trichostema* L. but were rare or absent in the other genera. Anisocytic stomata can be derived via several ontogenetic pathways (Payne, 1970). The ontogeny documented by Abu-Asab and Cantino (1987a) and shown in FIGURE 1, which if extended can give rise to helicocytic stomata (see below), is responsible for most or all of the stomata scored here as anisocytic. Superficially similar stomatal complexes that appeared to have been derived via other ontogenetic pathways (e.g., see Payne, 1970, *figs. 25–27*) were scored as anomocytic rather than anisocytic.

Helicocytic stomata, found in five genera of the Verbenaceae and two of the Prostanthereae but rarely in all species of a genus, occur only when anisocytic stomata are present and usually when they are the most common type. This association was also noted by Wilkinson (1979), and the ontogenetic connection between the two types has been documented by Payne (1970).

Paracytic stomata are widespread in the Verbenaceae, somewhat less widespread in subfam. Lamioideae, and very rare in subfam. Nepetoideae. They are particularly characteristic of *Prostanthera* Labill. and *Trichostema* in the Labiatae and of *Duranta* L., *Petraeovitex* Oliver, *Phyla*, *Oxera* Labill., and subfam. Symphorematoideae in the Verbenaceae. Payne (1970) commented that the paracytic type is ontogenetically the most variable stomatal complex in the dicotyledons. In the Labiatae and the Verbenaceae stomata scored as paracytic develop through at least two and perhaps more ontogenetic pathways. In the majority of genera where it is a common type, it appears to have an ontogeny whose initial steps are shared with the anisocytic stoma (see FIGURE 1). In other genera, in which anisocytic stomata are absent and diacytic and diallelocytic types are common, paracytic stomata may have an ontogeny similar to that of diacytic stomata (see FIGURE 1), differing only in the final division, the guard-cell mother cell dividing parallel to the subsidiary cells instead of perpendicular to them. This hypothesis is supported by the occurrence of occasional intermediates between diacytic and paracytic stomata, in which the guard cells lie at an oblique angle to the subsidiary cells (Pant & Kidwai, 1964; Inamdar & Bhatt, 1972). In *Sphenodesme* Jack and *Symphorema* Roxb. paracytic stomata are abundant and neither anisocytic nor diacytic types were found, suggesting that paracytic stomata may arise via a third, unknown pathway in these genera.

Actinocytic stomata are widespread in both the Labiatae and the Verbenaceae

but are seldom particularly common on a given leaf. The remaining three stomatal types were found in very few species: cyclocytic in three species of *Duranta*, staurocytic in *Lavandula multifida*, and parallelocytic in the three examined species of *Phyla*.

Amphistomatic leaves are slightly more frequent than hypostomatic ones in the Labiatae, but both conditions occur in every tribe (see TABLE 1). In contrast, over 70 percent of the species of Verbenaceae investigated, including all examined members of the Symphorematoideae, Callicarpeae, Petreeae, and Viticeae, and all but one species of the Caryopteridoideae and Citharexyleae, had hypostomatic leaves. Amphistomatic leaves predominate in the Chloanthoideae, Lantaneae, and Verbeneae. Variation within genera is common, both conditions being found in 20 genera of the Labiatae and five of the Verbenaceae. The difference between the Labiatae and the Verbenaceae in the proportion of species with each condition may be an ecological correlate. The Labiatae are much better represented than the Verbenaceae in arid and semiarid regions, and amphistomatic leaves tend to occur more commonly in xeric habitats (Parkhurst, 1978).

SUBSESSILE GLANDULAR TRICHOMES

Subsessile glandular trichomes have been widely reported in the Labiatae and the Verbenaceae under a variety of names, including peltate hairs, glandular dots, and glandular scales (Solereder, 1908; Metcalfe & Chalk, 1950; Huang & Cheng, 1971; Bosabalidis & Tsekos, 1982; Werker, Ravid, & Putievsky, 1985a). The adjective "subsessile" was applied by Abu-Asab and Cantino (1987a) because the glands may appear sessile in surface view but can be seen in cross section to have a short, usually discoid stalk cell (Fahn, 1979, *fig. 92*; Abu-Asab & Cantino, 1987a, *fig. 3*). The same term was employed for similar glands in the Acanthaceae by Ahmad (1978) and Karlström (1978, 1980). In many Labiatae the subsessile glands function in the secretion and storage of the essential oils (volatile terpenoids) that characterize the family (Fahn, 1979; Bosabalidis & Tsekos, 1982; Bruni & Modenesi, 1983; Werker, Ravid, & Putievsky, 1985a). Their ontogeny has been well documented (Bosabalidis & Tsekos, 1982, 1984; Bruni & Modenesi, 1983). Because subsessile glandular trichomes occur in nearly all Labiatae but vary in structure, they would seem to offer considerable potential as taxonomic characters. Abu-Asab and Cantino (1987a) developed a classification of subsessile gland types based on the number of cells and the cell-wall configurations in the head of the gland. This classification, modified to include a gland type found only in the Verbenaceae, has been adopted here (see FIGURE 2, APPENDIX).

Capitate glandular trichomes—i.e., those whose stalk is long in relation to the size of the head—are also widespread in the Labiatae but were not included in this survey because it was clear at the outset that they exhibit too much intrageneric variation to be of much use as phylogenetic indicators above the species level. Their presence complicated the scoring of subsessile gland types, however, because they occasionally intergrade. The intermediates have a stalk that is elongate rather than discoid but shorter than the head. As a rule of

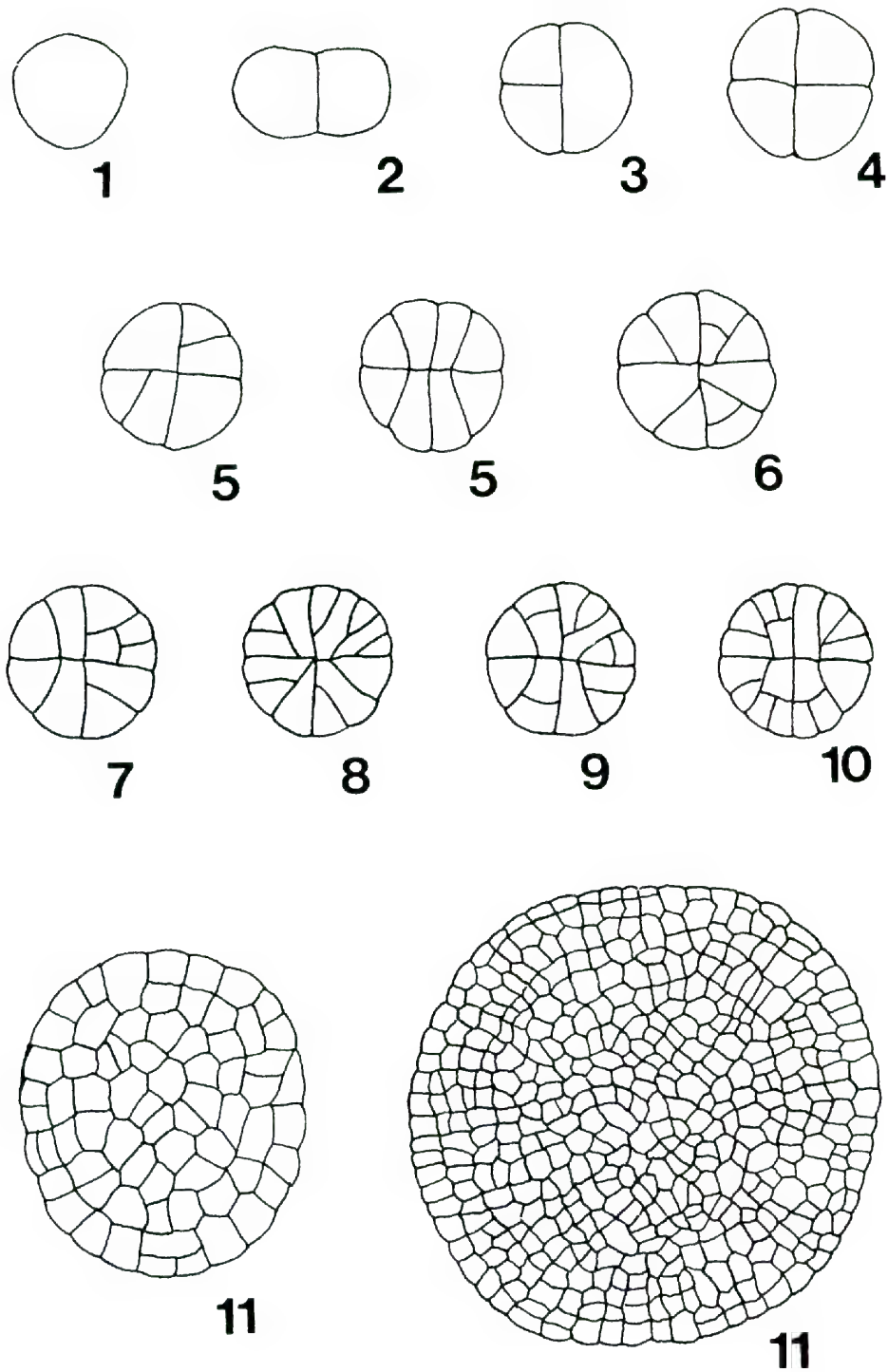


FIGURE 2. Examples of the 11 types of subsessile glandular trichomes in the Labiatae and Verbenaceae, as seen in surface view (see also APPENDIX).

thumb, these were counted as subsessile and included in TABLE 2 if the length of the stalk was no more than half the height of the head.

Subsessile glands are present in nearly all the Labiatae and Verbenaceae (see TABLE 2) but vary greatly in abundance. They are generally more common on the abaxial than the adaxial surface of the leaf. In some specimens only one or two glands were found in spite of much searching, and they were not found at all in three species of Verbenaceae (*Gmelina moluccana, Nesogenes dupontii, Premna octonervia*) and one of Labiatae (*Trichostema lanceolatum*). The glands occur in other species of each of these genera, and it is possible that they simply are very sparse in these four species and would be found if more leaves were examined. In *Trichostema lanceolatum* capitate glandular trichomes are abundant on the leaves and have been shown by Heisey and Delwiche (1984) to contain a phytotoxic essential oil. Thus the leaves of all examined species of Labiatae had glandular trichomes of some kind.

Types 4 and 5 were the most frequently observed subsessile glands in both families. Within the Verbenaceae type 4 was recorded in 78 percent and type 5 in 71 percent of the genera; within the Labiatae these figures were 76 and 72 percent, respectively (genera for which presence or absence could not be determined are excluded from percentage calculations here and elsewhere). In view of the frequency of type 4 glands in both families, their rarity in the Mentheae is noteworthy.

Type 2 glands are the third most frequent type in both families, occurring in 41 percent of the genera of Verbenaceae and 48 percent of the Labiatae, but at the tribal level they are less uniformly distributed than types 4 and 5. Type 2 glands are most common in subfam. Nepetoideae (except tribe Mentheae), tribe Lantaneae, and the genera *Ajuga* L., *Anisomeles* R. Br., *Eusteralis, Kinostemon* Kudo, *Leucas* R. Br., *Phlomis* L., *Pogostemon, Sideritis* L., and *Teucrium* L. in subfam. Lamioideae. They were infrequently encountered in subfam. Viticoideae and tribes Citharexyleae, Prostanthereae, and Mentheae and were not found at all in the Symphorematoideae or the Viticeae.

Type 1 glands were present in only six genera of Verbenaceae, four of them in the Lantaneae, but a wider distribution in the Verbenaceae was reported by Robert (1912; discussed below). In the Labiatae they were encountered frequently in tribe Mentheae and moderately so elsewhere in subfam. Nepetoideae. In subfam. Lamioideae they were found only in *Anisomeles, Eusteralis,* and *Pogostemon.*

Type 3 glands were observed in about a third of the genera of both families but were never very common when present, were rarely found in all examined species of a genus, and were only found when type 2 or 4 was present as well. Type 3 is probably an occasional derivative of the ontogenetic pathways that lead to types 2 and 4 glands and, as such, may be expected to occur irregularly in any species in which type 2 or 4 is common.

Type 6 glands are much more frequent in the Labiatae than in the Verbenaceae, where they were found in only ten genera, usually in only one species per genus. In the Labiatae they were most frequently present in subfam. Nepetoideae, although rare in tribe Ocimeae. In subfam. Lamioideae they were ob-

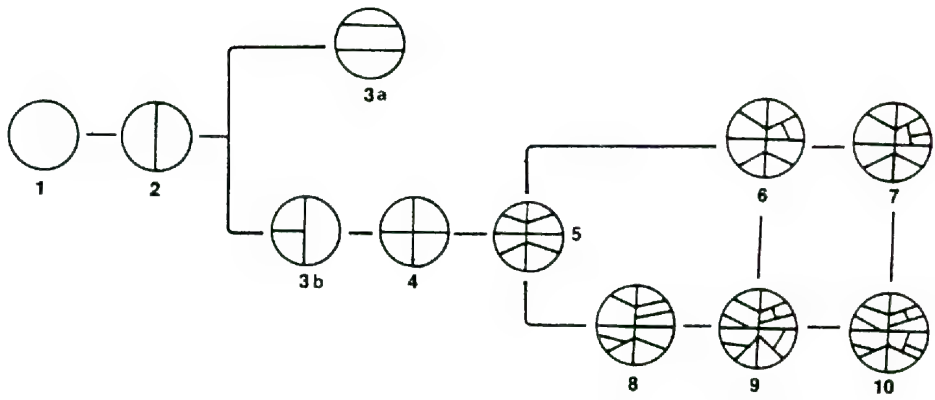


FIGURE 3. Hypothesized transformation series of subsessile glandular trichome types 1–10. (Figure originally published in Abu-Asab & Cantino, 1987a.)

served in over a third of the examined genera, but usually in only a single species.

Type 7 glands were found in nine species of Labiatae scattered through six tribes, no two species in the same genus. None were found in the Verbenaceae. Never common, type 7 glands occur only when type 6 is present as well and are best viewed as a rare derivative of the ontogenetic pathway that produces type 6 glands.

Type 8 glands were found in 11 genera of Verbenaceae and 20 of Lamioideae but in only one genus of Nepetoideae. They were seldom observed throughout a genus. The only genera in which type 8 glands appear to be characteristic (i.e., present in most or all examined species or, if only one species was examined, then the most common gland type in that species) are *Callicarpa* L. and *Citharexylum* L. in the Verbenaceae and *Brazoria* Engelm. ex A. Gray, *Craniotome* Reichb., *Cymaria* Bentham, *Prostanthera, Scutellaria,* and *Tinnea* Kotschy & Peyr. in the Labiatae.

Type 9 glands are also much more common in the Labiatae than in the Verbenaceae. In the Labiatae they occur most frequently in the Mentheae and least frequently in the Ajugeae, the Ocimeae, and the Pogostemoneae. Based on their structure, it appears that type 9 glands may arise via two different ontogenetic pathways: through the development of one or more tangential walls in what would otherwise be a type 8 gland, or the development of tertiary radial walls in what would otherwise be a type 6 gland (see FIGURE 3). Based on the co-occurrence of type 6 or 8 glands with type 9 it appears likely that type 9 glands have arisen via the type 6 pathway in subfam. Nepetoideae, where type 8 glands are very rare, as well as in some genera of the Lamieae. They have apparently arisen via the type 8 pathway in a scattering of Verbenaceae and Lamioideae (e.g., *Duranta, Tinnea*). However, there are many species in which type 9 glands are associated with both types 6 and 8 or neither, preventing indirect inference of the developmental pathway.

Type 10 glands were found in five species of Verbenaceae scattered among four genera. In the Labiatae they were encountered in about 20 percent of the

genera of both subfamilies but usually not throughout a genus. The only genera in which type 10 glands are "characteristic" (defined above in discussion of type 8 glands) are *Brazoria, Hemiandra* R. Br., and *Macbridea* Elliott ex Nutt. in the Labiatae and *Holmskioldia* Retz. in the Verbenaceae. In general, type 10 glands probably develop as an extension of the type 9 pathway (see FIGURE 3), but they may also develop from type 7 glands through the addition of tertiary radial walls. This may be the case in *Hemigenia saligna,* where types 7 and 10 glands occur but not type 9.

Type 11 glands are broad and scalelike, varying greatly in size even on a single leaf but always much larger than the other subsessile glands. Viewed with a dissecting microscope, they are yellowish or brownish and sometimes glistening (and therefore presumably glandular), but it is unclear whether they are fundamentally similar to the other subsessile gland types (hence their exclusion from FIGURE 3). They occur only in the Verbenaceae, where they were encountered in 30 percent of the genera but often in only one species per genus. They are most widespread in the Viticoideae and the Citharexyleae and were not found in the Chloanthoideae or the Verbeneae. Because they are sparse when present at all (rarely more than three seen on a slide), they may have been overlooked in some species and thus be of wider occurrence than TABLE 2 suggests. Glands of similar construction were documented by Robert (1912) in some species of *Clerodendrum, Duranta, Faradaya* F. Mueller, *Lippia* L., and *Stachytarpheta.* Their functional significance is unclear, but Fedorowicz (1916) referred to similar structures in *Melampyrum* L. (Scrophulariaceae) as extrafloral nectaries. Metcalfe and Chalk (1950) stated that extrafloral nectaries are common in *Clerodendrum.*

NONGLANDULAR TRICHOMES

Nonglandular trichomes were found in most species (see TABLE 2). Species with glabrous leaves (subsessile glandular trichomes are ignored in the definition of "glabrous" used here) were encountered in nearly a quarter of the genera of Verbenaceae examined but only one tenth of the genera of Labiatae. In the latter glabrousness is commonest in the Prostanthereae and rarest in the Ajugeae and the Nepetoideae.

The leaves of the vast majority of Labiatae and nonverbenoid Verbenaceae bear simple, multicellular (i.e., uniseriate) "hairs." The rarity of these trichomes in the Verbenoideae and the Prostanthereae is, in contrast, noteworthy. Excluding these two groups, nearly all other Verbenaceae and Labiatae that lack uniseriate hairs are either glabrous or bear branched, multicellular trichomes, which presumably evolved from uniseriate hairs. In most nonglabrous Prostanthereae and Verbenoideae, however, the hairlike trichomes are unicellular. Unicellular hairs are widespread in other groups of the Labiatae and the Verbenaceae as well; thus it is the absence of multicellular hairs in nonglabrous species rather than the presence of unicellular ones that characterizes the Verbenoideae and the Prostanthereae.

Branched, multicellullar trichomes were found in 20 percent of the genera of Verbenaceae and 16 percent of the genera of Labiatae examined. They are

TABLE 2. **Distribution of nonglandular trichomes and subsessile glands in Labiatae and Verbenaceae.**

Taxa[a]	Subsessile Glands[b] 1 2 3 4 5 6 7 8 9 10 11	Nonglandular[c] su sm bu bm
Lamiaceae		
"Lamioideae"		
"Ajugeae"		
Acrymia ajugiflora Prain	- * + + + - - - - - -	+ + - -
Ajuga chamaepitys (L.) Schreber	- * + + + - - - - - -	- + - -
A. genevensis L.	- + - - - - - - - - -	- + - -
A. laxmannii Benth.	- * - + - - - - - - -	- + - -
A. linearifolia Pampan.	- * + + + - - - - - -	+ + - -
A. reptans L.[§]	- * - + - - - - - - -	- + - -
A. sciaphila W.W.Smith	- * - + - - - - - - -	- + - -
Amethystea coerulea L. (#1)	- - - * + - - - - - -	+ + - -
A. coerulea L. (#2)	- - - * + - - - - - -	+ + - -
Cymaria dichotoma Benth.	- - - + + - - * - - -	+ + - -
Kinostemon ningpoensis (Hemsley) Kudo	- + + * - - - - - - -	- + - -
K. ornatum (Hemsley) Kudo (#1)	- * + * - - - - - - -	+ + - -
K. ornatum (Hemsley) Kudo (#2)	- + + * + - - - - - -	+ + - -
K. ornatum (Hemsley) Kudo (#3)	- + + * - - - - - - -	+ + - -
K. pernyi (Franchet) Kudo	- + + * + - - - - - -	+ + - -
Rubiteucris palmata (Benth. ex Hook.f.) Kudo	- + + * - - - - - - -	- + - -
Schnabelia oligophylla Hand.-Mazz.	- - + * - - - - - - -	- + - -
Tetraclea coulteri A.Gray (#1)	- - - + * - - - - + -	+ + - -
T. coulteri A.Gray (#2)	- - - * + - - - - - -	+ + - -
T. coulteri A.Gray (#3)	- - - + * - - - - + -	+ + - -
Teucrium arduinii L.	- + + * - - - - - - -	+ + - -
T. canadense L.[§]	- * + * + - - - - - -	- + - -
T. chamaedrys L.[§]	- * + * - - - - - - -	+ + - -
T. integrifolium F.Muell. ex Benth.	- + - * - - - - - - -	- + - -
T. laciniatum Torrey	- - - * + - - - - - -	+ + - -
T. marum L.	- + - * - - - - - - -	+ + - -
T. rotundifolium Schreber	- * - + + - - - - - -	- + - -
Tinnea aethiopica Kotschy ex Hook.f.(#1)	- - - - + - - * + - -	- + - -
T. aethiopica Kotschy ex Hook.f. (#2)	- - - + * - - - - - -	- + - -
T. antiscorbutica Welw.	- - - - + - - * - - -	+ + - -
T. apiculata W.Robyns & Lebrun	- - - - + - - ? ? ? -	+ + - -
T. galpinii Briq.	- - - - * + - + + - -	- + - -
T. rhodesiana S.Moore (#1)	- - - + + - - * + - -	+ + - -
T. somalensis Gurke ex Chiov.	- - - - + - - + * + -	+ + - -
Trichostema arizonicum A.Gray (#1)	- + + * + - - - - - -	+ + - -
T. arizonicum A.Gray (#2)	- + + * - - - - - - -	- + - -
T. brachiatum L.	- + - * + - - - - - -	+ + - -
T. dichotomum L.[§]	- - + * - - - - - - -	+ + - -
T. lanatum Benth.	- - - + * - - - - - -	- + - -
T. lanceolatum Benth.[§]	- - - - - - - - - - -	+ + - -
T. lanceolatum Benth.	- - - - - - - - - - -	+ + - -
T. setaceum Houtt.	- - - * - - - - - - -	- + - -
Lamieae		
Achyrospermum parviflorum S.Moore	- - - + * - - - - - -	- + - -
A. schimperi Perkins	- - - * + - - - - - -	- + - -
A. wallichianum Benth. ex Hook.f.	? ? ? * ? ? ? ? ? ? -	+ + - -
Acrotome fleckii (Gurke) Launert	- + - + * + + + + - -	+ + - -
A. hispida Benth.	- - - * + ? ? ? ? ? -	+ + - -
A. inflata Benth.	- - - * + - - - - - -	+ + - -

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b]											Nonglandular[c]			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
Ballota frutescens (L.) J.Woods	-	-	-	+	*	+	-	-	-	-	-	-	+	-	-
B. nigra L. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
B. pseudodictamnus (L.) Benth.	?	?	?	?	+	?	?	?	?	?	?	-	-	-	+
Brazoria arenaria Lundell[§]	-	-	-	+	*	-	-	+	+	+	-	-	+	-	-
B. pulcherrima Lundell[§]	-	-	-	+	*	-	-	+	+	+	-	-	+	-	-
B. scutellarioides Engelm. & A.Gray[§]	-	-	-	*	+	+	-	-	+	+	-	+	+	-	-
B. truncata (Benth.) Engelm. & A.Gray[§]	-	-	-	+	*	-	-	+	+	+	-	-	+	-	-
Chamaesphacos ilicifolius Schrenk	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-
Chelonopsis forrestii Anthony[§]	-	+	-	*	+	-	-	-	-	-	-	-	+	-	-
C. lichiangensis W.Smith	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
C. longipes Makino	-	-	-	+	+	+	-	-	+	-	-	-	+	-	-
C. odontochila Diels	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
Colquhounia coccinea Wallich	-	-	-	+	+	?	?	?	?	?	-	-	-	-	+
C. seguinii Vaniot	-	-	-	+	*	+	-	-	-	-	-	+	+	-	-
Craniotome furcata (Link) Kuntze	-	-	-	+	+	?	?	?	+	?	-	+	+	-	-
C. versicolor Reichb. (#3)	-	-	-	+	+	+	-	*	+	-	-	-	+	-	-
Eremostachys bachardenica B.Fedtsch.	-	-	-	+	+	-	-	-	-	-	-	-	+	-	-
E. iliensis Regel	-	*	+	+	-	-	-	-	-	-	-	-	+	-	-
E. labiosa Bunge	?	+	?	?	?	?	?	?	?	?	-	-	-	-	+
E. regeliana Aitch. & Hemsley	-	+	-	*	+	-	-	-	-	-	-	-	+	-	-
E. speciosa Rupr.	?	?	?	+	+	?	?	?	?	?	-	+	+	-	-
Eriophyton wallichianum Benth.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
Galeobdolon luteum Hudson[§]	-	-	-	*	+	+	-	-	+	-	-	-	+	-	-
Galeopsis ladanum L.	-	-	-	-	*	+	-	-	+	-	-	-	+	-	-
G. ochroleuca Lam.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
G. pubescens Besser	-	-	-	-	+	*	-	-	*	-	-	+	+	-	-
G. tetrahit L.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
Gomphostemma crinitum Wallich	-	-	+	*	+	-	-	-	-	-	-	+	+	-	+
G. javanicum (Blume) Benth.	-	-	-	+	?	?	?	?	?	?	-	-	+	-	+
G. lucidum Wallich	-	-	-	*	+	-	-	-	-	-	-	?	?	-	+
G. velutinum Benth.	?	?	?	?	+	?	?	?	?	?	?	-	+	-	+
Haplostachys haplostachya (A.Gray) St. John	-	*	+	-	-	-	-	-	-	-	-	-	+	-	-
H. linearifolia (Drake) Sherff	?	?	+	+	+	?	?	?	?	?	-	-	+	-	-
Lagochilus cabulicus Benth.	-	-	-	-	+	-	-	*	+	-	-	+	+	-	-
L. diacanthophyllus (Pallas) Benth.	?	?	?	+	+	?	?	+	+	?	-	+	+	-	-
L. ilicifolius Bunge	-	-	-	+	*	+	-	-	-	-	-	+	-	-	-
L. knorringianus Pavlov	-	-	-	-	-	-	-	-	*	+	-	+	-	-	-
L. platycalyx Fischer & C.Meyer (#2)	-	-	-	*	+	-	-	-	*	-	-	+	-	-	-
Lagopsis supina (Stephan) Ikonn.-Gal.	-	-	-	+	-	-	-	+	*	+	-	+	+	-	-
Lamiophlomis rotata (Benth.) Kudo	-	-	+	*	-	-	-	-	-	-	-	-	+	-	-
Lamium album L.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
L. maculatum L. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
L. maculatum L. (#2)	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
L. moschatum Miller	-	-	-	*	-	-	-	-	-	-	-	+	+	-	-
L. pictum Boiss. & Heldr.	-	-	-	*	+	+	-	-	+	-	-	+	+	-	-
L. purpureum L.[§]	-	+	+	*	+	+	-	-	-	-	-	+	+	-	-
Leonotis latifolia Gurke	-	-	-	-	*	+	-	-	+	-	-	-	+	-	-
L. leonitis R.Br.	-	-	+	+	*	-	-	-	-	-	-	-	+	-	-
L. leonurus (L.) R.Br. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
L. leonurus (L.) R.Br. (#2)	-	-	-	*	+	+	-	-	+	-	-	-	+	-	-

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b] 1	2	3	4	5	6	7	8	9	10	11	Nonglandular[c] su	sm	bu	bm
Leonurus cardiaca L.[§]	-	+	+	+	+	+	-	*	+	-	-	-	+	-	-
L. heterophyllus Sweet	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
Leucas altissima Engl.	-	+	-	+	*	-	-	-	-	-	-	-	+	-	-
L. capensis (Benth.) Engl.	-	+	+	*	+	-	-	-	-	-	-	?	+	-	-
L. ciliata Benth.	-	+	+	+	*	-	-	-	-	-	-	-	+	-	-
L. decemdentata R.Br.	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
L. mildbraedii Perkins	-	+	-	*	+	-	-	-	-	-	-	-	+	-	-
L. mollissima Wallich	?	?	?	*	?	?	?	?	?	?	-	+	+	-	-
Loxocalyx urticifolius Hemsley	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
Macbridea alba Chapman[§]	-	-	-	+	*	+	-	+	+	+	-	-	-	-	-
M. caroliniana (Walter) Blake[§]	-	-	-	+	*	*	-	-	+	+	-	-	-	-	-
Marrubium desertii Noë ex Cosson	-	-	-	+	*	-	-	-	-	-	-	-	-	-	+
M. peregrinum L.	-	+	+	*	+	-	-	-	-	-	-	-	-	-	+
M. vulgare L.	-	+	+	*	+	-	-	-	-	-	-	-	+	-	+
M. vulgare L.[§]	-	+	+	*	+	-	-	-	-	-	-	-	+	-	+
Melittis melissophyllum L.[§]	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
Metastachydium sagittatum (Regel) C.Y.Wu & Li	-	-	+	*	-	-	-	-	-	-	-	+	+	-	+
Microtoena insuavis (Hance) Prain ex Briq. (#1)	-	-	-	*	*	-	-	-	-	-	-	+	+	-	-
M. moupinensis Franchet ex Prain	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
M. robusta Hemsley	-	-	+	+	-	-	-	-	-	-	-	-	+	-	-
M. urticifolia Hemsley	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
Moluccella laevis L.	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-
M. spinosa L.	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
Notochaete hamosa Benth.	-	*	+	+	-	-	-	-	-	-	-	+	+	-	+
Otostegia aucheri Boiss.	-	-	-	*	+	-	-	-	*	+	-	+	+	-	-
O. integrifolia Benth.	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
O. limbata (Benth.) Benth. ex Hook.f.	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
O. persica (Burm.f.) Boiss.	-	-	-	+	*	+	-	+	-	-	-	-	+	-	-
Panzeria argyracea Kuprian.	?	?	?	+	?	?	?	?	?	?	-	-	+	-	-
Paraphlomis javanica (Blume) Prain ex Backer & Bakh.f.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
P. rugosa (Benth.) Prain	-	-	-	*	*	+	-	-	-	-	-	+	+	-	-
Phlomidoschema parviflorum (Benth.) Vved.	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
Phlomis agraria Bunge	-	*	-	*	-	-	-	-	-	-	-	+	+	-	+
P. bracteosa Royle	-	*	+	-	-	-	-	-	-	-	-	-	+	-	+
P. herba-venti L.	-	*	+	+	-	-	-	-	-	-	-	-	-	-	+
P. maximoviczii Regel	-	*	-	+	-	-	-	-	-	-	-	-	-	-	+
P. pratensis Karelin & Kir.	-	*	-	+	-	-	-	-	-	-	-	-	+	-	+
P. setigera Falc. ex Benth.	-	*	+	+	-	-	-	-	-	-	-	+	+	-	+
P. taurica Hartw. ex Bunge	?	+	?	?	?	?	?	?	?	?	?	-	-	-	+
P. tuberosa L.	-	*	-	-	-	-	-	-	-	-	-	-	+	-	+
P. umbrosa Turcz.	-	*	+	+	-	-	-	-	-	-	-	+	+	-	+
Phyllostegia brevidens A.Gray	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
P. grandiflora (Gaudich.) Benth. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
P. grandiflora (Gaudich.) Benth. (#2)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
P. hispida Hillebrand	-	-	-	+	*	+	-	+	+	-	-	-	+	-	-
P. lantanoides Sherff	-	-	+	*	-	-	-	-	-	-	-	+	+	-	-

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b]											Nonglandular[c]			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
Physostegia angustifolia Fern.[§]	-	-	-	*	+	-	-	+	+	+	-	-	-	-	-
P. digitalis Small[§]	-	-	-	+	*	-	-	-	-	-	-	-	-	-	-
P. godfreyi Cantino[§]	-	-	-	+	*	-	-	+	-	-	-	-	-	-	-
P. leptophylla Small[§]	-	-	-	*	+	+	-	-	-	-	-	-	-	-	-
P. longisepala Cantino[§]	-	-	-	*	+	-	-	-	-	-	-	-	-	-	-
P. purpurea (Walter) Blake[§]	-	-	-	+	*	-	-	-	-	-	-	-	-	-	-
P. virginiana (L.) Benth.[§]	-	-	-	*	+	-	-	-	+	+	-	-	-	-	-
Prasium majus L. (#1)	-	-	-	-	*	?	?	-	?	?	-	-	+	-	-
P. majus L. (#2)	-	-	-	-	*	-	-	-	+	-	-	-	-	-	-
Pseuderemostachys sewertzowii (Herder) Popov	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
Roylea calycina (Roxb.) Briq.	-	-	+	+	*	+	-	+	+	-	-	+	+	-	-
Sideritis hirsuta L.	-	+	-	+	+	+	-	+	*	+	-	-	+	-	-
S. ilicifolia Willd.	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
S. lagascana Willk.	-	*	-	+	+	*	-	-	-	-	-	+	+	-	-
S. lanata L.	-	*	+	+	-	-	-	-	-	-	-	-	+	-	-
S. montana L.	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
S. perfoliata L.	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
S. pullulans Vent.	-	*	+	+	+	-	-	-	-	-	-	-	+	-	-
S. romana L.	-	*	-	-	-	-	-	-	-	-	-	-	+	-	-
Stachyopsis oblongata (Schrenk) Popov & Vved.	-	-	-	*	-	-	-	-	-	-	-	+	+	-	-
Stachys acerosa Boiss.	-	-	-	+	+	+	?	?	?	?	-	+	+	-	-
S. annua (L.) L.	-	+	-	*	+	+	-	+	-	-	-	+	+	-	-
S. betonicaeflora Rupr.	-	+	-	+	*	+	-	+	+	-	-	+	+	-	+
S. coccinea Jacq.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
S. glutinosa L.	?	?	?	+	+	?	?	?	?	?	-	-	-	-	-
S. inflata Benth.	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
S. labiosa Bertol.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
S. riddellii House[§]	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
S. spathulata Burchell ex Benth.	?	+	+	+	?	?	?	?	?	?	-	-	-	-	+
S. spruneri Boiss. ex Benth.	-	*	-	+	-	-	-	-	-	-	-	+	+	-	-
S. tenuifolia Willd.[§]	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
Stenogyne diffusa A.Gray (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
S. diffusa A.Gray (#2)	-	-	-	*	-	-	-	-	-	-	-	+	+	-	-
S. kamehamehae Wawra	-	-	-	+	+	-	-	-	-	-	-	-	+	-	-
S. purpurea H.Mann	-	-	-	*	+	-	-	-	-	-	-	-	-	-	-
S. rugosa Benth.	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
Synandra hispidula (Michx.) Baillon[§]	-	-	-	*	+	+	+	-	+	-	-	-	+	-	-
Thuspeinanta brahuica (Boiss.) Briq.	-	-	-	-	+	*	-	-	+	-	-	-	+	-	-
T. persica (Boiss.) Briq.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Wiedemannia multifida (L.) Benth.	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
Pogostemoneae															
Colebrookea oppositifolia Smith (#1)	?	?	?	?	+	?	?	+	?	+	-	+	+	-	-
C. oppositifolia Smith (#2)	?	?	?	+	*	?	?	?	?	?	-	+	+	-	-
Comanthosphace stellipila S.Moore	-	-	-	+	*	-	-	-	-	-	-	-	+	-	+
C. sublanceolata (Miq.) S.Moore (#1)	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
C. sublanceolata (Miq.) S.Moore (#2)	-	-	-	+	*	-	-	-	-	-	-	-	+	-	+
Eusteralis cruciata (Benth.) Panigr.	+	*	-	-	-	-	-	-	-	-	-	+	+	-	-
E. sampsonii (Hance) Panigr.	?	+	?	?	?	?	?	?	?	?	-	-	-	-	-
E. stellata (Lour.) Panigr. (#1)	*	+	-	-	-	-	-	-	-	-	-	-	-	-	-
E. stellata (Lour.) Panigr. (#2)	+	*	-	-	-	-	-	-	-	-	-	+	-	-	-

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b] 1	2	3	4	5	6	7	8	9	10	11	Nonglandular[c] su	sm	bu	bm
Pogostemon auricularius (L.) Hassk.	*	*	-	-	-	-	-	-	-	-	-	-	+	-	-
P. brachystachyus Benth.	*	+	-	-	-	-	-	-	-	-	-	-	+	-	-
P. cablin (Blanco) Benth.	*	*	-	-	-	-	-	-	-	-	-	+	+	-	-
P. elsholtzioides Benth.	*	+	-	-	-	-	-	-	-	-	-	+	+	-	-
P. glaber Benth. (#1)	*	*	-	-	-	-	-	-	-	-	-	-	+	-	-
P. glaber Benth. (#2)	*	*	-	-	-	-	-	-	-	-	-	-	+	-	-
P. heyneanus Benth.[§]	*	*	-	-	-	-	-	-	-	-	-	-	+	-	-
P. plectranthoides Desf.	*	*	-	-	-	-	-	-	-	-	-	+	+	-	-
Rostrinucula dependens (Rehder) Kudo	-	-	-	+	*	+	-	-	-	-	-	-	-	-	+
R. sinensis (Hemsley) C.Y.Wu	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
Prostanthereae															
Hemiandra pungens R.Br.	-	-	-	-	-	-	-	-	+	*	-	-	-	-	-
Hemigenia incana Benth. (#1)	-	-	+	*	-	-	-	-	-	-	-	-	+	-	-
H. incana Benth. (#2)	-	+	+	*	+	-	-	-	-	-	-	-	+	-	-
H. saligna Diels	-	-	-	-	-	+	+	-	-	*	-	+	-	-	-
Microcorys brevidens Benth.	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
Prostanthera cuneata Benth.	-	-	-	?	?	?	?	+	?	?	-	-	-	-	-
P. lasianthos Labill. (#1)	-	-	-	-	*	?	?	?	?	?	-	-	-	-	-
P. lasianthos Labill. (#2)	-	-	-	-	*	+	?	*	+	?	-	-	-	-	-
P. nivea Cunn. ex Benth. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	-	-	-
P. nivea Cunn. ex Benth. (#2)	-	-	+	*	+	-	-	+	-	-	-	+	-	-	-
P. ovalifolia R.Br.	-	-	-	+	+	?	?	+	?	?	-	-	-	-	-
P. rotundifolia R.Br.[§]	-	-	+	+	?	?	?	*	?	?	-	-	-	-	-
P. rotundifolia R.Br.	-	-	-	+	?	?	?	+	?	?	-	-	-	-	-
P. saxicola R.Br.	-	-	+	*	-	-	-	-	-	-	-	+	-	-	-
Westringia amabilis J.Boivin	-	-	-	-	+	*	-	+	+	-	-	-	-	-	-
W. cheelii Maiden & Betche	-	-	-	-	-	-	-	-	?	+	-	+	-	-	-
W. fruticosa (Willd.) Druce	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-
Scutellarieae															
Salazaria mexicana Torrey (#1)	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
S. mexicana Torrey (#2)	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
Scutellaria amoena C.H.Wright	-	-	-	-	*	+	-	+	+	-	-	+	+	-	-
S. elliptica Muhlenb.[§]	-	-	-	*	-	-	-	+	-	-	-	-	+	-	-
S. gardoquioides Benth.	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
S. hirtella Juz.	?	?	?	+	+	?	?	?	?	?	-	-	+	-	-
S. incana Biehler[§]	-	-	-	+	+	+	-	*	+	-	-	+	+	-	-
S. integrifolia L.[§]	-	-	-	+	*	-	-	+	-	-	-	+	+	-	-
S. lateriflora L.[§]	-	+	+	*	-	-	-	-	-	-	-	-	+	-	-
S. multicaulis Boiss.	-	-	+	+	*	+	-	+	+	-	-	+	+	-	-
S. nervosa Pursh[§]	-	-	-	*	+	-	-	+	-	-	-	+	+	-	-
S. ovata Hill[§]	-	-	+	*	+	+	-	+	-	-	-	-	+	-	-
S. serrata Andrz.[§]	-	+	+	*	+	-	-	-	-	-	-	-	+	-	-
Uncertain Tribal Affin.															
Ajugoides humilis (Miq.) Makino (#1)	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
A. humilis (Miq.) Makino (#2)	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
Anisomeles heyneana Benth.	*	+	+	-	-	-	-	-	-	-	-	-	+	-	-
A. indica (L.) Kuntze (#1)	*	+	-	-	-	-	-	-	-	-	-	+	+	-	-
A. indica (L.) Kuntze (#2)	*	+	-	-	-	-	-	-	-	-	-	-	+	-	-
A. malabarica (L.) R.Br. ex Sims (#1)	*	+	-	-	-	-	-	-	-	-	-	-	+	-	-
A. malabarica (L.) R.Br. ex Sims (#2)	*	+	-	-	-	-	-	-	-	-	-	-	+	-	-
Eurysolen gracilis Prain (#1)	-	-	+	+	+	+	?	+	+	?	-	-	+	-	-
E. gracilis Prain (#2)	?	?	?	?	+	+	?	?	?	?	-	+	+	-	-
Hypogomphia turkestana Bunge	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-
Leucosceptrum canum Smith	?	?	?	+	?	?	?	?	?	?	?	-	-	-	+
Suzukia shikikunensis Kudo	?	?	?	+	+	?	?	?	?	?	-	-	+	-	-

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b] 1 2 3 4 5 6 7 8 9 10 11	Nonglandular[c] su sm bu bm
Nepetoideae		
"Mentheae"		
Ceratominthe odora (Griseb.) Hauman	* - - - ? + ? ? ? ? -	+ + - -
Cyclotrichium origanifolium (Labill.) Manden. & Scheng.	- - - - - * - - + + -	- - - -
Elsholtzia fruticosa (D.Don) Rehder	- * + ? ? ? ? ? + ? -	+ + - +
E. patrinii (Lepechin) Garcke	- * - ? ? ? ? ? + ? -	+ + - -
Hedeoma graveolens Chapman ex A.Gray	- - - - - * + - + + -	+ + - -
H. nanum (Torrey) Briq.	* - - - + ? ? ? ? ? -	+ + - -
Keiskea japonica Miq.	- - - - * ? ? ? ? ? -	+ + - -
Lepechinia hastata (A.Gray) Epling	+ - - - * + - - - - -	- - - +
Lycopus americanus Muhlenb.	- + - + * - - - - - -	+ + - -
L. rubellus Moench	? ? - - * - - - - - -	+ + - -
L. virginicus L.	- * - + + - - - - - -	+ + - -
Melissa officinalis L. (#1)	- - - - * * - - + - -	+ + - -
Mentha arvensis L.	? ? ? ? ? + ? ? ? ? -	+ + - -
M. citrata Ehrh.	? ? ? ? + ? ? ? ? ? -	- + - -
M. piperita L.	? ? ? ? + + ? ? ? ? -	- + - -
Monardella odoratissima Benth.	+ - - - - + + - * + -	+ + - -
M. villosa Benth.	+ - - - ? * ? ? + ? -	+ + - -
Perillula reptans Maxim. (#1)	- * + - * - - - - - -	+ + - -
P. reptans Maxim. (#2)	+ * - - + ? ? ? ? ? -	+ + - -
Pogogyne zizyphoroides Benth.	+ - - - + - - - - - -	+ - - -
Poliomintha glabrescens A.Gray ex Hemsl.	* - - - * ? ? ? ? ? -	+ + - -
Pycnanthemum floridanum E.Grant & Epling	- - - - * ? ? ? ? ? -	+ + - -
P. aff. incanum (L.) Michaux	- - - - * ? ? ? ? ? -	+ + - -
Rhododon ciliatus (Benth.) Epling	* - - - + ? ? ? ? ? -	- + - -
Satureja arkansana (Nutt.) Briq.	* - - - * + ? ? ? ? -	+ - - -
S. douglasii (Benth.) Briq.	* - - - + * - - + - -	+ + - -
S. parvifolia (Philippi) Epling	* - - - ? * ? ? + ? -	+ + - -
S. popovii B.Fedtsch. & Gontch.	+ - - - - * - - + - -	+ + - -
Thymus serpyllum L.	+ ? ? ? ? + ? ? ? ? -	+ + - -
Nepeteae		
Agastache breviflora (A.Gray) Epling	- + - - + + ? + ? ? -	- + - -
A. cana (Hook.) Wooton & Standley	- * - - ? + ? ? + ? -	+ + - -
A. nepetoides (L.) Kuntze	? ? ? ? + ? ? ? ? ? -	+ + - -
A. pallidiflora (A.A.Heller) Rydb.	? * ? ? + ? ? ? ? ? -	+ + - -
Cedronella canariensis (L.) Webb & Berth. (#1)	- - - - - + ? ? + + -	+ + - -
Dracocephalum heterophyllum Benth.	- * - + - + + - - - -	+ + - -
D. parviflorum Nutt.	? + ? ? + ? ? ? ? ? -	+ + - -
D. ruyschiana L.	- * - - + + - - - - -	+ + - -
Glechoma hederacea L.	- * - - + + - - - - -	+ + - -
Lophanthus chinensis Benth.	* + - - - - - - - - -	+ + - -
Meehania cordata (Nutt.) Britton	? ? ? + ? + ? ? ? ? -	+ + - -

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b]											Nonglandular[c]			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
Nepeta cataria L.	-	*	-	+	+	-	-	-	-	-	-	-	+	-	-
N. clarkei Hook.f.	-	+	-	-	+	*	+	-	-	-	-	-	+	-	-
N. curviflora Boiss.	?	+	?	+	?	?	?	?	?	?	-	-	+	-	-
N. discolor Royle ex Benth.	?	?	?	?	+	+	?	?	?	?	-	+	+	-	-
N. nepetella L.	-	*	-	+	+	-	-	-	-	-	-	+	+	-	-
Prunella vulgaris L.	+	*	-	-	-	-	-	-	-	-	-	-	+	-	-
Ocimeae															
Acrocephalus fruticosus Dunn	-	+	-	-	+	*	+	-	*	+	-	+	+	-	+
A. indicus Kuntze	-	*	-	+	-	-	-	-	-	-	-	+	+	-	-
Becium obovatum (E.Meyer) N.E.Br.	*	-	-	*	-	-	-	-	-	-	-	-	+	-	-
Capitanya otostegioides Gurke	?	?	?	?	+	+	?	?	?	?	-	-	+	-	-
Catopheria capitata Benth. ex Hemsley (#1)	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
C. capitata Benth. ex Hemsley (#2)	+	*	-	+	-	-	-	-	-	-	-	-	+	-	-
C. chiapensis A.Gray ex Benth.	*	*	-	+	-	-	-	-	-	-	-	+	+	-	-
Endostemon obtusifolius (E.Meyer) N.E.Br.	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
Eriope crassipes Benth.	?	?	?	+	?	?	?	?	?	?	-	-	+	-	-
Eriopidion strictum (Benth.) R.Harley	?	*	-	+	-	-	-	-	-	-	-	+	+	-	-
Fuerstia africana T.C.E.Fries	?	+	?	+	+	?	?	?	?	?	-	-	+	-	-
Haumaniastrum callianthum (Briq.) R.Harley	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
H. coeruleum (Oliver) Duvign. & Plancke	-	*	-	*	-	-	-	-	-	-	-	-	+	-	-
Hemizygia canescens (Gurke) Ashby	-	*	-	-	-	-	-	-	-	-	-	+	+	-	-
Holostylon katangense W.Robyns et Lebrun	-	*	-	*	-	-	-	-	-	-	-	+	+	-	-
H. strictipes G.Taylor	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
Hyptis alata (Raf.) Shinn.	-	-	-	*	-	-	-	-	-	-	-	+	+	-	-
H. emoryi Torrey	?	?	?	+	?	?	?	?	?	?	?	-	-	-	+
H. mutabilis (Rich.) Briq.	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
H. oblongifolia Benth.	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
Icomum lineare Burkill	+	*	+	?	?	?	?	?	?	?	-	-	-	-	-
Lavandula multifida L.	-	+	+	*	+	-	-	-	-	-	-	+	+	-	+
L. stoechas L.	-	*	-	?	+	-	-	-	-	-	-	-	-	-	+
Nautochilus labiatus (N.E.Br.) Bremek.	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
Ocimum americanum L.	-	*	-	+	-	-	-	-	-	-	-	+	+	-	-
O. basilicum L.	-	*	+	*	-	-	-	-	-	-	-	+	+	-	-
O. gratissimum L. (#1)	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
O. gratissimum L. (#2)	+	+	-	*	-	-	-	-	-	-	-	+	+	-	-
Orthosiphon affinis N.E.Br.	*	+	-	-	-	-	-	-	-	-	-	-	+	-	-
O. aristatus (Blume) Miq.	-	*	-	+	-	-	-	-	-	-	-	+	+	-	-
O. diffusus Benth.	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
Plectranthastrum clerodendroides T.C.E Fries	?	+	?	?	+	?	?	?	?	?	-	+	+	-	-
Plectranthus forsteri Benth.	-	?	-	+	+	-	-	-	-	-	-	+	+	-	-
P. scutellarioides (L.) R.Br.	-	*	+	+	-	-	-	-	-	-	-	-	+	-	-

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b] 1	2	3	4	5	6	7	8	9	10	11	Nonglandular[c] su	sm	bu	bm
Rabdosia excisa (Maxim.) H.Hara	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
R. inflexa (Thunb.) H.Hara	-	-	+	*	-	-	-	-	-	-	-	-	+	-	-
R. nervosa (Hemsley) C.Y.Wu & Li	-	+	+	*	-	-	-	-	-	-	-	-	+	-	-
Rabdosiella calycina (Benth.) Codd	-	+	+	*	+	-	-	-	-	-	-	-	+	-	-
Solenostemon scutellarioides (L.) Codd (#1)	-	+	-	*	+	-	-	-	-	-	-	+	+	-	-
S. scutellarioides (L.) Codd (#2)	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
Syncolostemon densiflorus Benth.	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
"Salvieae"															
Arischrada bucharica (Popov) Pobed.	-	*	-	-	-	+	+	-	+	+	-	-	+	-	-
Blephilia hirsuta (Pursh) Benth.[§]	-	-	-	?	+	?	?	?	?	?	-	+	+	-	-
Monarda clinopodia L.	?	+	?	?	+	?	?	?	?	?	-	-	+	-	-
M. fistulosa L.[§]	?	?	?	?	+	?	?	?	?	?	-	+	+	-	-
M. punctata L.	?	?	?	?	+	?	?	?	?	?	-	+	+	-	-
Perovskia abrotanoides Karelin	+	+	+	+	+	*	-	-	*	*	-	+	-	-	+
P. atriplicifolia Benth.	-	*	+	+	+	+	-	-	+	-	-	-	-	-	+
Rosmarinus officinalis L.	?	?	?	?	?	?	?	?	?	?	?	?	?	-	+
Salvia carnosa Douglas	-	-	-	+	*	+	-	-	-	-	-	+	-	-	-
S. farinacea Benth.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
S. reflexa Hornem.	-	*	-	*	+	-	-	-	-	-	-	-	+	-	-
Verbenaceae															
Avicennioideae															
Avicennia nitida Jacq.	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
Caryopteridoideae															
Caryopterideae															
Caryopteris divaricata (Siebold & Zucc.) Maxim.	?	?	?	+	+	?	?	?	?	?	-	-	+	-	-
C. forrestii Diels (#1)	?	?	?	*	?	?	?	?	?	?	-	+	+	-	-
C. forrestii Diels (#2)	?	?	?	*	?	?	?	?	?	?	-	+	+	-	-
C. grata Benth.	-	+	-	+	*	-	-	-	-	-	-	-	+	-	-
C. incana (Thunb.) Miq. (#2)	?	+	?	+	?	?	?	?	?	?	-	+	+	-	-
C. mongholica Bunge (#2)	?	?	?	+	?	?	?	?	?	?	-	?	+	-	-
C. nepetaefolia (Benth.) Maxim.	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
C. odorata (Ham.) Robinson	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
C. terniflora Maxim.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
Glossocarya siamensis Craib	-	+	+	+	*	+	-	-	-	-	-	+	+	-	-
Peronema canescens Jack	?	?	?	+	?	?	?	?	?	?	?	+	+	-	-
Petraeovitex kinabaluensis Munir	-	-	-	+	*	-	-	-	-	-	-	-	-	-	-
P. multiflora (Smith) Merr.	-	-	-	-	*	+	-	+	+	-	+	-	-	-	-
Teijsmanniodendreae															
Teijsmanniodendron ahernianum (Merr.) Bakh.	-	-	-	+	+	-	-	-	+	*	-	-	+	-	-
T. subspicatum (H.Hallier) Kosterm.	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-
Chloanthoideae															
Achariteae															
Nesogenes dupontii Hemsley	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-
N. euphrasioides (Hook. & Arn.) A.DC.	-	-	-	-	+	-	-	-	-	-	-	+	+	-	-
Pityrodia atriplicina (F.Muell.) Benth.	?	?	+	+	?	?	?	?	?	?	?	-	-	-	+
P. dilatata (F.Muell.) Benth.	?	?	?	+	+	?	?	?	?	?	?	-	-	-	+
P. paniculata (F.Muell.) Benth.	-	*	+	-	-	-	-	-	-	-	-	-	-	-	+

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b] 1 2 3 4 5 6 7 8 9 10 11	Nonglandular[c] su sm bu bm
Spartothamnella puberula (F.Muell.) Maiden & Betche (#1)	? ? ? + ? ? ? ? ? ? -	+ + - +
S. puberula (F.Muell.) Maiden & Betche (#2)	- + + * - - - - - - -	+ + - +
S. puberula (F.Muell.) Maiden & Betche (#3)	- + - * - - - - - - -	+ + - +
Chloantheae		
Chloanthes stoechadis R.Br.	? ? ? ? ? ? ? ? ? ? ?	- + - +
Cyanostegia angustifolia Turcz.	? ? ? ? + ? ? ? ? ? ?	- - - -
C. microphylla S.Moore	? ? ? ? + ? ? ? ? ? ?	- + - -
Physopsideae		
Dicrastylis exsuccosa (F.Muell.) Druce	- * + + ? ? - - - - -	- - - +
Lachnostachys eriobotrya (F.Muell.) Druce	? ? ? ? ? ? ? ? ? ? ?	- - - +
Mallophora globiflora Endl.	? ? ? ? ? ? ? ? ? ? ?	- - - +
Newcastelia cephalantha F.Muell.	* - - - - - - - - - -	- - - +
Nyctanthoideae		
Nyctanthes arbor-tristis L.	+ + + * + - - - - - -	+ - - -
Phrymoideae		
Phryma leptostachya L.	- * - - - - - - - - -	- + - -
Symphorematoideae		
Congea chinensis Mold.	- - - * + - - - - - -	+ + - -
C. forbesii King & Gamble	- - - * - - - - - - +	- + - -
C. tomentosa Roxb.	- - - * + - - - - - -	- + - +
Sphenodesme ferruginea (Griffith) Briq.	? ? ? ? ? ? ? ? ? ? -	- + - +
S. pentandra Jack	- - - + * - - - - - +	- + - -
Symphorema luzonicum (Blanco) Fernandez-Villar	? ? ? + ? ? ? ? ? ? ?	- - - -
Verbenoideae		
Citharexyleae		
Citharexylum affine D.Don	- - - - * - - - - - +	+ - - -
C. berlandieri Robinson	- - - - * - - + + - -	+ - - -
C. caudatum L.	- - - - * + - + + - -	+ - - -
C. ligustrinum Van Houtte	- - - - + - - * - - -	- - - -
C. punctatum Greenman	- - - - * - - * + - -	+ - - -
Duranta mandonii Mold.	- - - - + - - * + - -	- + - -
D. mutisii L.f.	- - - - + - - + * + +	? ? - -
D. peruviana Mold.	- - - - * ? ? ? ? ? -	- + - -
D. repens L. (#1)	- - - + * - - - - - +	+ + - -
D. repens L. (#2)	- - - + * - - - - - +	- + - -
Rehdera trinervis (S.F.Blake) Mold.	- * - + - - - - - - -	- - - -
Rhaphithamnus spinosus (A.L.Juss.) Mold.	- - + * - - - - - - +	+ - - -
Lantaneae		
Aloysia gratissima (Gill. & Hook.) Tronc.	* - - + - - - - - - -	+ - - -
A. wrightii (A.Gray) A.A.Heller	* - - - - - - - - - -	+ - - -
Bouchea prismatica (L.) Kuntze	- * + + + - - - - - -	+ - - -
Diostea juncea (Gillies & Hook.) Miers	? ? ? ? ? ? ? ? ? ? ?	+ - - -
Lantana horrida Kunth (#1)	+ * + + + - - - - - -	+ - - -
L. horrida Kunth (#2)	+ * - + + - - - - - -	+ - - -
L. involucrata L.	* + - + - - - - - - -	+ - - -

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b] 1	2	3	4	5	6	7	8	9	10	11	Nonglandular[c] su	sm	bu	bm
Lippia graveolens Kunth	*	+	-	-	-	-	-	-	-	-	-	+	-	-	-
Phyla incisa Small	?	?	?	?	?	?	?	?	?	?	?	-	-	+	-
P. lanceolata (Michaux) E.Greene[§]	*	+	-	+	-	-	-	-	-	-	-	-	-	+	-
P. nodiflora (L.) E.Greene	?	+	?	+	?	?	?	?	?	?	-	-	-	+	-
Priva aspera Kunth	-	*	-	+	-	-	-	-	-	-	-	+	-	-	-
P. grandiflora (Ortega) Mold.	-	*	+	+	+	-	-	-	-	-	-	+	-	-	-
Stachytarpheta frantzii Polak.	-	*	-	-	-	-	-	-	-	-	-	+	+	-	-
S. jamaicensis (L.) Vahl	-	-	+	*	-	-	-	-	-	-	-	-	-	-	-
Monochileae															
Amasonia campestris (Aublet) Mold.	-	-	-	+	*	-	-	-	-	-	+	+	+	-	-
A. hirta Benth.	?	?	?	+	+	?	?	?	?	?	+	-	+	-	-
Petreeae															
Gasselia hymenocalyx Briq.	-	*	-	-	-	-	-	-	-	-	-	+	-	-	-
Petrea arborea Kunth	?	?	?	+	?	?	?	?	?	?	-	+	-	-	-
P. volubilis L. (#1)	-	-	-	+	*	-	-	-	-	-	-	+	-	-	-
P. volubilis L. (#2)	-	-	-	+	*	-	-	-	-	-	-	+	-	-	-
Recordia boliviana Mold.	?	?	?	?	?	?	?	?	?	?	?	+	+	-	-
Verbeneae															
Glandularia bipinnatifida (Nutt.) Nutt.	-	-	-	*	-	-	-	-	-	-	-	+	-	-	-
G. canadensis (L.) Small	-	-	-	*	-	-	-	-	-	-	-	+	-	-	-
Hierobotana inflata (Kunth.) Briq.	?	?	?	?	?	?	?	?	?	?	?	+	-	-	-
Junellia ligustrina (Lagascana) Mold.	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-
Tamonea curassavica (L.) Pers.	-	*	-	+	+	-	-	-	-	-	-	+	-	-	
Verbena hastata L.[§]	-	-	-	+	*	-	-	-	-	-	-	+	-	-	-
V. litoralis Kunth	?	?	?	+	?	?	?	?	?	?	-	+	-	-	-
V. macdougalii A.A.Heller	-	-	+	*	-	-	-	-	-	-	-	+	-	-	-
V. pumila Rydb.	-	-	-	*	-	-	-	-	-	-	-	+	-	-	-
V. urticifolia L.[§]	-	-	+	*	+	-	-	+	-	-	-	+	-	-	-
Viticoideae															
Callicarpeae															
Aegiphila aculeifera Mold.	-	-	-	-	*	+	-	+	+	-	-	-	+	-	-
A. deppeana Steudel	-	-	+	+	*	-	-	-	-	-	-	-	+	-	-
A. pendula Mold.	-	+	+	*	+	-	-	-	-	-	+	+	+	-	-
Callicarpa americana L.	-	-	-	+	+	+	-	*	+	-	+	-	+	-	+
C. dichotoma (Lour.) K.Koch	-	-	-	+	+	-	-	*	+	+	+	+	+	-	-
C. mollis Siebold & Zucc.	?	?	?	+	?	?	?	?	?	?	?	+	+	-	+
Geunsia farinosa Blume	?	?	?	?	?	?	?	?	?	?	-	+	+	-	+
Clerodendreae															
Clerodendrum aculeatum (L.) Schldl.	-	-	-	+	*	-	-	?	?	?	-	-	+	-	-
C. anafense Britton & P.Wilson	-	-	-	-	*	+	-	-	-	-	+	-	+	-	-
C. capitatum (Willd.) Schum. & Thonn.	-	-	-	-	+	?	?	?	?	?	-	-	+	-	-
C. cuneatum Gurke	-	-	-	+	*	-	-	-	-	-	-	-	+	-	+
C. floribundum R.Br.	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-
C. glabrum E.Meyer	-	-	-	-	*	-	-	+	-	-	-	-	-	-	-
C. inerme (L.) Gaertner	-	-	+	*	+	-	-	-	-	-	-	-	+	-	-
C. philippinum Schauer	-	-	-	+	*	-	-	-	-	-	+	+	+	-	-
C. squiresii Merr.	-	+	+	*	+	-	-	-	-	-	+	-	+	-	-
Faradaya amicorum (Seemann) Seemann	-	-	-	-	*	+	-	-	-	-	-	-	-	-	-
F. splendida F.Muell.	?	?	?	?	+	+	?	?	?	?	-	-	-	-	-

TABLE 2. (*continued*).

Taxa[a]	Subsessile Glands[b] 1 2 3 4 5 6 7 8 9 10 11	Nonglandular[c] su sm bu bm
Holmskioldia sanguinea Retz. (#1)	- - - - + - - - * - -	- + - -
H. sanguinea Retz. (#2)	- - - - * - - + * + -	- + - -
H. sanguinea Retz. (#3)	- - - - + - - + * + -	- + - -
H. tettensis (Klotzsch) Vatke	- - - - + + - - * + -	+ + - -
Kalaharia spinescens Gurke	- - - - * - - + - - +	+ + - -
Karomia fragrans Dop	- - - * + - - - - - -	- - - -
Oxera morierii Vieill.	- - - - - + - * - - -	- - - -
O. neriifolia Beauv.	- - + * + - - - - - +	- - - -
O. sulfurea Dubard	- - - + * - - - - - -	- - - -
Teucridium parvifolium Hook.f.	- + + * - - - - - - -	- + - -
Tectoneae		
Petitia domingensis Jacq.	- - - * + - - - - - -	- + - -
Viticeae		
Cornutia grandiflora (Cham. & Schldl.) Schauer	? ? ? ? + ? ? ? ? ? -	- + - -
C. pyramidata L.	- - + * + - - - - - +	+ + - -
Garrettia siamensis Fletcher	- - - + * - - - - - +	- + - -
Gmelina delavayana Dop	? ? + + + ? ? ? ? ? +	- - - -
G. moluccana (Blume) Backer	- - - - - - - - - - -	+ + - -
Premna barbata Wallich	- - - - * + - + - - -	- + - -
P. corymbosa Willd.	- - - - - * - - + - -	+ + - -
P. foetida Reinw.	- - - - * - - - - - -	- + - -
P. japonica Miq.	- - - - * + - + + - -	- + - -
P. octonervia Merr. & Metcalf	- - - - - - - - - - -	- - - -
Pseudocarpidium avicennioides (A.Rich.) Millsp.	? ? ? + ? ? ? ? ? ? -	+ - - -
P. wrightii Millsp.	- - - * - - - - - - -	- - - -
Tsoongia axillariflora Merr.	- - - + * - - - - - -	+ + - -
Vitex agnus-castus L.	- - - * - - - - - - -	+ + - -
V. cannabifolia Siebold & Zucc.	- - - * + - - - - - -	+ + - -

[a]If name is followed by the symbol §, data are from Abu-Asab and Cantino (1987a). All other data are from the present survey. #1, #2, etc. refer to different specimens of a species; the numbers correspond to entries in the voucher list deposited in four major botanical libraries (see Materials and Methods).

[b]Subsessile Gland Types defined in Appendix 1. Symbols: *, commonest type(s); +, present; -, absent; ?, unknown whether present or absent (glands are poorly stained or obscured by dense trichomes).

[c]Nonglandular Trichomes: su, simple unicellular; sm, simple multicellular (uniseriate); bu, branched unicellular; bm, branched multicellular. Symbols: +, present; -, absent; ?, presence uncertain.

most widespread in the Chloanthoideae and were not observed in the Verbenoideae, Ajugeae, Prostanthereae, Scutellarieae, or Nepeteae. However, Robert (1912) reported them in some species of *Citharexylum* (Verbenoideae), and within the Prostanthereae they are known from two species of *Prostanthera* (Conn, 1984) and at least two species of *Hemigenia* R. Br. (Bentham, 1870; B. Conn, pers. comm.). Outside the Chloanthoideae, genera whose leaves are

characteristically clothed with branched, multicellular trichomes include *Comanthosphace, Gomphostemma* Bentham, *Leucosceptrum, Marrubium* L., *Perovskia* Karelin, *Phlomis,* and *Rostrinucula* (see TABLE 2; Bokhari & Hedge, 1971; Azizian & Cutler, 1982; Press, 1982). Branched, unicellular (two-armed) trichomes were found only in *Phyla.*

DISCUSSION

SAMPLE SIZE LIMITATIONS

Because this survey was motivated by an interest in phylogenetic relationships among genera and suprageneric groups, particularly within subfam. Lamioideae and related Verbenaceae, taxonomic breadth of coverage was emphasized at the expense of depth. Very few species are represented by more than a single specimen. Consequently, the data in the tables should not be used to characterize species or infer interspecific relationships, although they may suggest avenues for further research in certain genera. However, the sample sizes for many genera of Lamioideae and for suprageneric groups in both families are sufficient to provide a general picture of the distribution of trichome and stomatal types in the Lamiales.

In most genera of subfam. Nepetoideae, the number of species sampled is too low to be any more than suggestive about the epidermal anatomy of the genus. Although perhaps disappointing to those whose primary interest lies in this subfamily, the shallow sampling of this group is justifiable in relation to the ultimate objective of the survey—an improved understanding of the origin of the Labiatae and of relationships among its basal clades (which lie within the paraphyletic or polyphyletic subfam. Lamioideae). Although subfam. Nepetoideae includes well over half the genera of Labiatae, it represents but a single clade (Cantino & Sanders, 1986) whose closest relatives lie somewhere within subfam. Lamioideae. Knowledge of its character-variation pattern is therefore no more nor less critical to an understanding of the origin and early evolution of the Labiatae than is that of any single genus in the Lamioideae.

COMPARISON WITH PUBLISHED DATA

There has been no broad survey of the morphology of trichomes in the Labiatae or the morphology of stomata in the Verbenaceae. El-Gazzar and Watson (1968) investigated stomatal configurations in a wide range of Labiatae but listed only the predominant type in each genus. Furthermore, their observations regarding many genera of the Lamioideae conflict markedly with my own (discussed below). Robert's (1912) study of trichome morphology in the Verbenaceae provides extensive data on the nonglandular trichomes and capitate glandular trichomes of some 55 genera, but the descriptions and illustrations of the more complex subsessile glands (except type 11) are, for the most part, inadequate to classify them according to the system used here. Nonetheless, the study is a useful complement to the present one in that the nonglandular trichomes are described in far more detail than they are in this paper. Moreover,

Robert included 11 genera in his survey that are not covered here, most of them in the Chloanthoideae and the Stilboideae.

In addition to these two surveys, some information is available on individual genera or groups of genera (Labiatae—Mayer (1909), Bech (1963), Kaleva (1967), Wieffering (1970), Bokhari & Hedge (1971, 1976), Inamdar & Bhatt (1972), Heinrich (1973), Rudall (1980, 1986), Azizian & Cutler (1982), Press (1982), Sharma & Shome (1982), Bruni & Modenesi (1983), Manzanares *et al.* (1983), Shah & Naidu (1983), Bosabalidis & Tsekos (1984), Werker, Putievsky, & Ravid (1985), Werker, Ravid, & Putievsky (1985a, b); Verbenaceae—Mullan (1931), Pant & Kidwai (1964), Kundu & De (1968), Inamdar (1969a), Ramayya & Rao (1969), Inamdar *et al.* (1976), Fahn & Shimony (1977), Puff (1978), Trivedi & Upadhyay (1978), Bhatt *et al.* (1979), Mathew & Shah (1981, 1983), Shah & Mathew (1982a, b)).

By and large, the data provided in these publications are consistent with those reported here, but some disagreements and additions to the data base warrant discussion. Robert (1912) reported type 1 subsessile glands in nine genera of the Verbenaceae in which I either failed to find them (*Avicennia* L., *Casselia* Nees & C. Martius, *Dicrastylis* J. L. Drumm. ex Harvey, *Petitia* Jacq., *Priva* Adanson, *Stachytarpheta*, and *Verbena* L.) or could not determine whether they were present or absent (*Peronema* Jack), or that I did not study (*Hemiphora* F. Mueller). Type 1 glands were reported in *Avicennia* by Mullan (1931) as well, but not in the very thorough study by Fahn and Shimony (1977), so this discrepancy probably represents genuine intrageneric variation rather than error. In the Labiatae type 1 glands have been reported from some species of *Phlomis* (Bech, 1963; Azizian & Cutler, 1982), a genus in which I failed to find them, as well as from numerous genera of subfam. Nepetoideae (see below).

Studies of the subsessile glands of tribe Mentheae (Mayer, 1909; Kaleva, 1967; Bruni & Modenesi, 1983; Bosabalidis & Tsekos, 1984; Werker, Putievsky, & Ravid, 1985; Werker, Ravid, & Putievsky, 1985a), including five genera not examined here, confirm that the group is characterized by the absence of type 4 glands and the presence of both type 1 glands and those with tangential walls (usually types 6 and/or 9). Type 1 glands were also reported from the majority of the Ocimeae studied by Shah and Naidu (1983) and in subtribe Hyptidinae (Ocimeae) by Rudall (1980). In tribe Salvieae glandular trichomes that appear to be type 1 have been reported in *Dorystaechas* Boiss. & Heldr. ex Bentham, *Horminum* L., *Meriandra* Bentham, *Perovskia*, *Salvia* L., and *Zhumeria* Rech. f. & Wendelbo (Bech, 1963; Bokhari & Hedge, 1971, 1976; Sharma & Shome, 1982). Thus type 1 glands occur widely in subfam. Nepetoideae and may be better thought of as characterizing this more inclusive group rather than tribe Mentheae alone.

It is difficult to evaluate the apparent conflicts in the distribution of stomatal types in the Verbenaceae—among published works and between some of them and the present study—because of differences in how authors classified the stomatal complexes. For example, Mathew and Shah (1981) reported anisocytic stomata in more genera of Verbenaceae than I have, but upon examination of their illustrations, it appears that they have classified as anisocytic many stomata that I would have scored as anomocytic—stomata that happen to be in

contact with three surrounding cells, but these (some or all of them) not distinguishable from the other epidermal cells. Several other stomatal types (e.g., haplocytic, tetracytic) recognized by Shah and Mathew in this and other papers (1982a, b) were also treated as anomocytic in the present study. On the other hand, stomata that I would have scored as actinocytic are treated by Mathew and Shah as anomocytic in some cases and cyclocytic in others.

In spite of these classification problems, which apply mainly to the papers by Shah and Mathew, published illustrations provide some genuine additions to the data base. Stomata that I would have scored as anisocytic are documented for seven genera in which I did not record them (*Bouchea, Gmelina* L., *Petrea* L., *Phyla, Premna,* and *Stachytarpheta*) or that I did not study (*Tectona* L. f.) (Pant & Kidwai, 1964; Inamdar *et al.,* 1976; Bhatt *et al.,* 1979; Mathew & Shah, 1981). In addition, diacytic stomata have been recorded from *Citharexylum, Gmelina,* and *Nyctanthes* L. (Trivedi & Upadhyay, 1978; Bhatt *et al.,* 1979; Mathew & Shah, 1981), paracytic from *Nyctanthes, Premna,* and *Tectona* (Inamdar *et al.,* 1976; Trivedi & Upadhyay, 1978; Mathew & Shah, 1981), and cyclocytic from a few species of *Clerodendrum* (Shah & Mathew, 1982a).

With regard to the Labiatae, there is universal agreement that the diacytic types of stomata (including diallelocytic) predominate in subfam. Nepetoideae, but El-Gazzar and Watson's (1968, 1970) observations on subfam. Lamioideae conflict markedly with my own. The data in Table 1 do not support their assertion (1970, p. 476) that if *Prunella* L., *Cleonia* L., and the North American Melittidinae are excluded, anomocytic stomata "are the rule" in Bentham's "Stachydeae" (Lamieae). Both diacytic and anomocytic stomata occur in all examined genera of the group thus circumscribed by El-Gazzar and Watson (i.e., excluding *Prunella,* etc.), and diacytic stomata are as or more common than anomocytic in about two thirds of them. Furthermore, El-Gazzar and Watson (1968) listed *Achyrospermum* Blume, *Acrotome* Bentham ex Endl., *Ajuga, Anisomeles, Comanthosphace, Craniotome, Galeobdolon* Adanson, *Gomphostemma, Moluccella* L., *Phyllostegia* Bentham, *Rostrinucula, Sideritis, Thuspeinanta* T. Durand, and *Wiedemannia* Fischer & C. Meyer (not all in Bentham's Lamieae) as having predominantly anomocytic and/or anisocytic stomata, whereas I found diacytic and/or diallelocytic stomata to be commonest in these genera and did not find anisocytic stomata in any of them.

Phylogenetic Significance

This is one of several character surveys being conducted in preparation for a cladistic analysis of the Lamiales. Although the phylogenetic significance of the data in Tables 1 and 2 can best be assessed in the context of such an analysis, Hennigian reasoning can be applied to single characters to yield tentative suggestions about their significance. Thus if it can be shown that a character state is derived in a particular group, it may be treated as a potential synapomorphy for a clade within that group unless the distribution of other characters indicates that such a conclusion is unparsimonious. This approach will be employed here.

Outgroup comparison (Watrous & Wheeler, 1981; Maddison *et al.,* 1984)

will be used to assess character polarity. It is generally recognized that the Labiatae arose from the Verbenaceae (Cronquist, 1981), which is consequently paraphyletic, but the affinities of the Labiatae are difficult to identify more precisely. Pollen morphology (Raj, 1983) and gynoecial structure (Junell, 1934) suggest that the closest relatives of the Labiatae lie within the Viticoideae and/or the Caryopteridoideae and that the Verbenoideae are unlikely to be closely related. The other subfamilies, except perhaps the Chloanthoideae, seem to have little in common with the Labiatae. In evaluating the polarity and phylogenetic significance of characters within the Labiatae, one must therefore pay particular attention to their occurrence in the Viticoideae and the Caryopteridoideae.

The Scrophulariales is the best-supported sister group of the Lamiales (Cantino, 1982; Frohlich, 1987) and will be treated here as the sole outgroup. More distant outgroups will not be considered because higher-level relationships in the Asteridae are poorly resolved. The distributions of stomatal and trichome types are reasonably well documented in the Acanthaceae (De, 1967; Ahmad, 1974, 1978; Karlström, 1978, 1980) and the Gesneriaceae (Rosser & Burtt, 1969; Van Cotthem, 1971; Sahasrabudhe & Stace, 1974; Herat & Theobald, 1979; Yuen & Dehgan, 1982; Wiehler, 1983), but extensive surveys have not been published for the other families of Scrophulariales. In the discussion that follows, statements about the epidermal anatomy of these families are based on the summaries provided by Solereder (1908) and Metcalfe and Chalk (1950), the distributions of stomatal types tabulated by Wilkinson (1979), and studies of particular genera or groups of genera (Bignoniaceae—Paliwal (1970), Jain (1978), Elias & Newcombe (1979), Henrickson (1985); Lentibulariaceae—Casper (1966), Komiya (1972), Trinta (1979), Fineran (1985); Myoporaceae—Dell & McComb (1977); Pedaliaceae (including Martyniaceae)—Mullan (1936), Inamdar (1969b), Karatela & Gill (1984); Plantaginaceae—Andrzejewska-Golec & Swietoslawski (1987); Scrophulariaceae—Fedorowicz (1916), Spoerri (1930), Bhatt & Inamdar (1975), Stefanova-Gateva & Boeva (1979), Doaigey & Harkiss (1982), Henrickson & Flyr (1985)).

Anomocytic stomata, found in all examined species of Verbenaceae and nearly all Labiatae, are the most widespread stomatal type in the Scrophulariales as well, occurring commonly in every family except the Acanthaceae (absent) and the Plantaginaceae (rare). Hence the hypothesis that their presence is ancestral (and their absence derived) in the Labiatae is parsimonious, regardless of whether the Labiatae are monophyletic or polyphyletic and of which groups of Verbenaceae are most closely related to the Labiatae. It is also worth noting that presence/absence of anomocytic stomata exhibits less intrageneric variation than most other characters in this study and is therefore of particular value in assessing intergeneric phylogenetic relationships. In tribe Lamieae anomocytic stomata are universally present in 42 of the 45 investigated genera and universally absent in the other three (*Brazoria, Macbridea,* and *Physostegia* Bentham). Absence of anomocytic stomata is thus a corroborating synapomorphy for a clade proposed by Abu-Asab and Cantino (1987a) comprising these three genera. It may be of some phylogenetic significance in subfam.

Nepetoideae as well, but the much poorer sample of this subfamily makes evaluation difficult.

Diallelocytic stomata are common in the Acanthaceae but rare to absent in the other families of the Scrophulariales. If the Acanthaceae were the basal clade of the Scrophulariales, polarity of this character within the Lamiales would be equivocal. However, assuming the Acanthaceae are not basal (a reasonable assumption; see Cronquist, 1981), it is most parsimonious to hypothesize that absence of diallelocytic stomata is the ancestral condition in the Lamiales and that their presence is derived. The three-celled diallelocytic type is of special interest as the only epidermal feature whose distribution parallels relatively closely the traditional boundary between the families; i.e., it is very common in the Labiatae but infrequent in the subfamilies of the Verbenaceae that appear to be most closely related to them. Its phylogenetic significance is discussed below (see Circumscription of Labiatae). Four-celled diallelocytic stomata can be hypothesized to represent a derived state as well, again assuming that the Acanthaceae is not the basal family of the Scrophulariales, but because this character exhibits far more intrageneric variation than the previous one, it is of little phylogenetic significance above the genus level.

In the Scrophulariales cyclocytic stomata have been reported only from the Bignoniaceae, where they are apparently infrequent. Their presence in three of the four examined species of *Duranta* is therefore hypothesized to be derived. The other species (*D. repens*) has quite a different set of stomatal types (anisocytic and helicocytic but not cyclocytic), a distinction that might be of systematic value within the genus and warrants further study. It should be noted, though, that many stomata in the former three species of *Duranta* have an incomplete or irregular circle of subsidiary cells and thus seem to be intermediate between anomocytic and cyclocytic. Study of stomatal ontogeny in this genus is needed before any systematic conclusions are drawn. Two other rare stomatal types, staurocytic and parallelocytic, also appear to be derived states and of possible phylogenetic significance, the former at the species level within *Lavandula* L. and the latter as a synapomorphy for *Phyla*.

The distributions of the other stomatal types are of limited phylogenetic value above the genus level because of difficulties in assessing polarity, questions of homology, and/or high intrageneric variability. Actinocytic stomata have been reported only a few times in the Scrophulariales (in a few members of the Bignoniaceae, Gesneriaceae and Lentibulariaceae), but it is unclear whether they are genuinely rare or have been classified as anomocytic by most authors. Moreover, the ontogeny of actinocytic stomata in the Lamiales is unknown; thus they cannot necessarily be considered homologous in the taxa where they occur. A more definite homology problem exists in the case of paracytic stomata, which appear to develop via several different ontogenetic pathways in the Lamiales (discussed above).

Anisocytic stomata are the predominant type in the Gesneriaceae; they also occur at least occasionally in the Bignoniaceae, Scrophulariaceae, Pedaliaceae, and Myoporaceae but never in the other families of Scrophulariales. Hence it is unclear whether presence or absence is ancestral in the Lamiales. Similarly,

diacytic stomata are common in the Acanthaceae and the Plantaginaceae, at least occasional in the Lentibulariaceae, the Pedaliaceae, and the Scrophulariaceae, and rare to absent in the other families of the Scrophulariales. Again, polarity in the Lamiales cannot be assessed without knowing something about cladistic topology within the Scrophulariales. Nor can polarity be assessed within the Labiatae, because both anisocytic and diacytic stomata occur widely, but far from universally, in the two subfamilies of the Verbenaceae that are thought to be closest to them. This is unfortunate, because the two characters exhibit relatively little intrageneric variation within the Labiatae and an intriguing, inversely correlated distribution pattern. In the Prostanthereae and two genera of the Ajugeae (*Tetraclea* and *Trichostema*), diacytic stomata are rare while anisocytic stomata are nearly universally present and often the most common stomatal type. In the rest of the Ajugeae and all gynobasic-styled Labiatae, the reverse is true. From a phenetic standpoint at least, these characters neatly distinguish the Prostanthereae from the gynobasic-styled Labiatae and also give cause to question whether *Tetraclea* and *Trichostema* belong in the family (further discussed below). The inverse correlation between anisocytic and diacytic stomata is weaker in the Verbenaceae, where many genera have neither, and a few (e.g., *Holmskioldia* and *Lantana*) have both. The group of Verbenaceae in which anisocytic stomata are most consistently present is subfam. Chloanthoideae. Their absence in *Nesogenes* A. DC., which also lacks the branched trichomes characteristic of the Chloanthoideae (see below), is consistent with its exclusion from this group (as by Marais, 1981).

Stomatal position (leaves hypostomatic vs. amphistomatic) is of little value as a phylogenetic indicator because of its high intrageneric variability, the existence of an intermediate condition with a few stomata on the adaxial surface of the blade, and the apparent correlation with environmental factors (discussed above). This correlation appears to hold in the Scrophulariales as well: hypostomatic leaves predominate in the families best represented in the humid tropics (Acanthaceae, Gesneriaceae, Bignoniaceae), while amphistomatic ones are commonest in those well represented in xeric habitats (Myoporaceae, Pedaliaceae, Plantaginaceae). Both conditions occur widely in the Scrophulariaceae.

Subsessile glands, nearly universally present in the Labiatae and the Verbenaceae, are equally characteristic of the Scrophulariales, where they are frequent in all families except the Myoporaceae and the Plantaginaceae. Type 4 is the most common type in the Scrophulariales and therefore probably represents an ancestral condition in the Lamiales, where it was found in more than three quarters of the genera of both families. The absence of type 4 glands in nearly all examined Mentheae can thus reasonably be hypothesized to be a derived state and may be of help in circumscribing this poorly defined tribe. The character's value as a phylogenetic indicator is reduced, however, by its relatively high intrageneric variability elsewhere in the Labiatae and the Verbenaceae. Subsessile glandular trichomes of types 1, 2, and 5 are also quite widespread in the Scrophulariales but are not so universal as to permit polarity assessment in the Lamiales.

The more complex gland types (6–11) are generally rare in the Scrophulariales (except that type 11 is widespread in the Bignoniaceae). It is reasonable to

hypothesize that all are derived in the Lamiales. However, these characters exhibit so little constancy within genera (and sometimes even within species; e.g., types 8 and 9 in *Tinnea aethiopica,* types 8 and 10 in *Holmskioldia sanguinea*) that their phylogenetic significance above the species level is probably minimal. Moreover, types 9 and 10 may arise through more than one ontogenetic pathway (see FIGURE 3 and associated text) and are thus not necessarily homologous where they do occur. In view of these problems, the presence of type 10 glands in all species of *Brazoria* and *Macbridea* and some species of *Physostegia,* invoked by Abu-Asab and Cantino (1987a) in support of a clade composed of these three genera, must be considered very weak evidence. This clade is more convincingly supported by the absence of anomocytic stomata, as discussed above.

Nonglandular trichomes, both simple-unicellular and uniseriate, occur widely in the Scrophulariales, the latter type being found in nearly all nonglabrous members of the order. The presence of both kinds of "hairs" is thus probably ancestral in the Lamiales. There is a great deal of intrageneric variation in presence vs. absence of unicellular trichomes in the Lamiales, but much less so for uniseriate trichomes. The rarity of uniseriate trichomes in the Verbenoideae is therefore of interest. Presence of *only* unicellular hairs (i.e., absence of uniseriate hairs in nonglabrous species) may represent a synapomorphy, and the taxonomic position of the few genera of Verbenoideae in which uniseriate trichomes were observed (*Amasonia, Duranta, Recordia* Mold., *Stachytarpheta*) should be examined. Indeed, the pollen morphology of *Amasonia* (but not of the other three genera) suggests that it belongs with the Viticoideae or the Caryopteridoideae rather than the Verbenoideae (Raj, 1983). The rarity of multicellular foliar hairs in the Verbenoideae has also been noted by Robert (1912) and El-Gazzar (1974). This character may be of phylogenetic significance in the Prostanthereae as well, but with over half the examined species being glabrous, the sample size of those with hairs of any kind was too small to draw any conclusions.

Branched, multicellular trichomes occur in a scattering of genera in the Scrophulariales but are not common in the major families; they are unlikely to be ancestral in the Lamiales. Their presence in most Chloanthoideae may be a synapomorphy for a large subgroup composed of all genera except *Nesogenes.* (Although the foliage of *Cyanostegia* Turcz. is glabrous or nearly so, branched hairs are present on the ovaries and fruits (Munir, 1978).) Presence of branched, multicellular trichomes is also a probable synapomorphy uniting the species of individual genera such as *Phlomis* and *Perovskia*—genera that, on the basis of other characters, are unlikely to be closely related to each other. Unicellular, two-armed trichomes occur in one genus of Acanthaceae (Solereder, 1908) but are clearly a derived condition in the Lamiales, where they represent a synapomorphy of *Phyla.*

CIRCUMSCRIPTION OF THE LABIATAE

This study was originally undertaken in the hope that it might contribute to an understanding of phylogenetic relationships among the basal clades of the

Labiatae. Several stomatal characters have turned out to be of interest in this regard. As discussed above, the presence of diallelocytic stomata can reasonably be hypothesized to be a derived state. As such, it would seem to support a clade composed of the gynobasic-styled Labiatae (i.e., subfam. Nepetoideae, subfam. Lamioideae tribes Lamieae, Pogostemoneae, and Scutellarieae, and the genera of "uncertain tribal affinities" in TABLE 1) plus *Acrymia* Prain, *Ajuga, Cymaria, Kinostemon, Rubiteucris* Kudo, and *Teucrium* of the Ajugeae. In the Verbenaceae diallelocytic stomata were found in seven genera of subfam. Verbenoideae, two of Caryopteridoideae, and two of Viticoideae (see TABLE 1). On the basis of pollen and gynoecial morphology (Junell, 1934; Raj, 1983), the Verbenoideae are unlikely to be closely related to the Labiatae, so the occurrence of diallelocytic stomata in this group is probably due to parallelism. A close phylogenetic relationship between one or more of the other verbenaceous genera in which diallelocytic stomata occur (i.e., *Caryopteris* (sect. *Pseudocaryopteris* Briq. only), *Clerodendrum* (subg. *Cyclonema* only), *Petraeovitex,* and *Premna*) and the Labiatae that share this derived state is somewhat more plausible but may be unparsimonious when other characters are considered.

Although diallelocytic stomata were not found in all species of the Lamieae, Scutellarieae, and Nepetoideae, they occur in the vast majority of the members of these three groups, each of which is defined as a clade on the basis of other (nonepidermal) characters. The presence of diallelocytic stomata is thus a "nonuniversal derived state" shared by a set of clades and, as argued by Cantino (1985), provides evidence for a larger clade composed of them. The critical requirements are that the state be derived and that the groups united on the basis of it each be supported as a clade by other characters. A shared, nonuniversal derived state constitutes weaker evidence of phylogenetic relationship than a shared, universal derived state—i.e., one found throughout the groups it unites (Cantino, 1985).

The distributions of anisocytic and diacytic stomata exhibit a pattern that is highly congruent with that of the diallelocytic stomata, although it is not known whether presence or absence of the former two types is derived. In the Labiatae with a gynobasic style and most Ajugeae, anisocytic stomata are rare and diacytic stomata are nearly universally present. All three stomatal characters (two of them used only in a phenetic sense, since their polarity cannot be assessed) delimit a group composed of all gynobasic-styled Labiatae plus some Ajugeae. Tribe Prostantheree is consistently excluded from this group, as are *Tetraclea* and *Trichostema* of tribe Ajugeae. Among the other Ajugeae, all three characters support the inclusion of *Acrymia, Ajuga, Cymaria, Kinostemon,* and *Rubiteucris.* The stomatal characters conflict or are ambiguous with regard to the other four genera. *Schnabelia* Hand.-Mazz. has diacytic stomata, but the slide was too poor to determine whether anisocytic or diallelocytic stomata were present as well. In *Amethystea* L. diacytic stomata are present, diallelocytic stomata absent, and anisocytic stomata rare. *Teucrium* consistently has diacytic and diallelocytic stomata, but anisocytic ones were found in two species. *Tinnea* consistently has diacytic stomata and lacks diallelocytic; anisocytic stomata were found in one species only. The strong positive correlation between the occurrences of diacytic and diallelocytic stomata is hardly

surprising since the initial steps in their ontogenies are the same (Payne, 1970), but there is no reason to expect the observed negative correlation between diacytic and anisocytic stomata. Indeed, this correlation is much weaker in the Verbenaceae.

The relationships suggested by these characters must be evaluated in the light of others, and recircumscription of the Labiatae at this time would be highly premature. However, those taxa whose epidermal anatomy is divergent from the rest of the Labiatae should be carefully examined. One of these (*Tetraclea*) has been assigned to the Verbenaceae by some authors (e.g., Moldenke, 1971), and the flowers of another (*Trichostema*) bear a striking resemblance to those of *Caryopteris* sect. *Pseudocaryopteris* in the Verbenaceae. The supratectal spinelike projections on the pollen of *Tetraclea* (Raj, 1983) and *Trichostema* (Abu-Asab & Cantino, 1989), as well as a few other genera of Ajugeae, constitute a derived feature shared by many Verbenaceae (Raj, 1983) and entirely unlike the exine sculpturing of the gynobasic-styled Labiatae (Abu-Asab & Cantino, 1987b).

The Prostanthereae have traditionally been placed in the Labiatae because the ovary is moderately lobed (with the style somewhat sunken but not gynobasic) and matures to form four nutlets. However, the characteristic suite of stomatal types in the Prostanthereae, with anisocytic stomata abundant in all but one genus (they are present but uncommon in *Westringia* Smith), diacytic stomata rare, and diallelocytic stomata absent, differs markedly from that in the gynobasic-styled Labiatae and resembles certain groups of Verbenaceae—particularly subfam. Chloanthoideae and tribe Clerodendreae. This is intriguing from a biogeographic standpoint since the Prostanthereae and most genera of Chloanthoideae are Australian endemics, while the Labiatae (other than Prostanthereae) are rather poorly represented in Australia (Bentham, 1870). In a numerical phenetic analysis of Labiatae and Verbenaceae (El-Gazzar & Watson, 1970), the Prostanthereae, Chloanthoideae, and Stilboideae clustered together tightly. It is not clear that the similar suites of stomatal types in the Prostanthereae and Chloanthoideae reflect cladistic relationship, since absence of diallelocytic stomata is an ancestral state and the polarity of the other two characters cannot be assessed without knowing more about cladistic topology of the Verbenaceae and/or the Scrophulariales, but the possibility that these two Australian groups may be more closely related than generally thought warrants study.

ACKNOWLEDGMENTS

I gratefully acknowledge the technical assistance of Jon Hamer, who improved upon the clearing and staining procedure previously used in our lab and prepared the vast majority of the slides. Some slide preparation was also carried out by Gregory Rhinehalt. FIGURE 2 was drawn by Rebecca Samson, and FIGURES 1 and 3, reprinted from an earlier paper in the *Journal of the Arnold Arboretum,* were originally prepared by Mones Abu-Asab. I thank the curators of the Harvard University Herbaria, the Missouri Botanical Garden, the New York Botanical Garden, and the U. S. National Herbarium for permission to

remove leaf material for study. I am grateful to Paula Rudall for introducing me to the Royal Botanic Garden's computerized data base of anatomical literature, which greatly facilitated my literature survey of the Lamiales and Scrophulariales, and to Ray Harley for his generosity with his time and facilities during my stay at Kew, where the manuscript was prepared. This research was supported by National Science Foundation Grant BSR 83-06878 (Principal Investigator, P. D. Cantino) and Ohio University Baker Fund Award 88-10.

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APPENDIX 1. **Classification of subsessile glandular trichomes in the Labiatae and Verbenaceae.***

TYPE 1. Head composed of one cell.

TYPE 2. Head composed of two cells.

TYPE 3. Head divided by three radial walls to form three cells, one twice as large as the other two.

TYPE 4. Head composed of four cells.

TYPE 5. Head of more than four cells, usually divided by four primary radial walls that are more or less perpendicular to each other; tertiary and tangential walls absent; no more than one secondary radial wall arising on a given side of any primary radial wall.

TYPE 6. As in type 5, but with tangential walls present; partial and tertiary radial walls absent.

TYPE 7. As in type 6, but with partial radial walls present.

TYPE 8. Head of more than four cells; tertiary radial walls present and/or more than one secondary radial wall arising on the same side of at least one primary radial wall; tangential walls absent.

TYPE 9. As in type 8, but with tangential walls present; partial radial walls absent.

TYPE 10. As in type 9, but with partial radial walls present.

TYPE 11. More complex than type 10, with many tangential walls forming concentric layers of cells.

*Illustrated in FIGURE 2; adapted from Abu-Asab and Cantino (1987a).

ON THE GENUS BURRETIODENDRON SENSU LATO (TILIACEAE)[1]

REN ZHUGE[2]

Burretiodendron Rehder is a small tiliaceous genus with six species, limitedly distributed in southwestern China, northern Vietnam, Burma, and Thailand. Although much research has been carried out on this taxon since 1936, there are still a number of problems both in taxonomy and morphology requiring further clarification. The new evidence weighs against the separation of *Excentrodendron* from *Burretiodendron*. *Burretiodendron* is an isolated taxon that appears to be related to *Sicrea* Hallier f. and *Schoutenia* Korth. on the basis of pollen morphology. The distribution pattern of the group suggests that it may have originated near the China-Vietnam border.

Burretiodendron, a small genus of six species, is distributed from southwestern China through Tonkin to northern peninsular Thailand and Burma. Most species of the genus are restricted to the border area of southern China and northern Vietnam, where they grow primarily on limy soils in rain forests or dry deciduous woods.

Burretiodendron is most readily distinguished from the other genera of the Tiliaceae by its characteristic flowers and fruits, but due to the diversity of its habitat and flower types, mistakes in observation are easy to make, particularly when material is limited. Chang and Miau (1978) divided the genus into two genera, *Burretiodendron* sensu stricto and *Excentrodendron* Chang & Miau, on the basis of incomplete observations. *Excentrodendron* was described as having bisexual flowers and an evergreen habit and as being distinct from *Burretiodendron* s.s. I have checked almost all the specimens of both taxa kept in Chinese herbaria, as well as photographs of some specimens housed in other countries. The specimen cited under *Excentrodendron tonkinense* (A. Chev.) H. T. Chang & R. H. Miau as evidence of its bisexual flowers is *China–Soviet Union Expedition 2618,* from Jinping county of southwestern Yunnan; it bears juvenile fruits with several stamens at the base. Although the flower really is bisexual, the specimen is definitely *B. esquirolii.* Additional studies on flower type indicate that most species of both *Burretiodendron* s.s. and *Excentrodendron* are monoecious or dioecious, with only *B. esquirolii* being monoecious or polygamous. My observations show that *B. kydiifolium* Hsu & Zhuge retains its old leaves until the new ones unfold the following spring. It is possible that the habitats of *B. siamense* Kosterm. and *B. brilletii* Kosterm. are similar to

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Journal of the Arnold Arboretum **71**: 371–380. July, 1990.

that of *B. kydiifolium* because the leaves of all three species are more or less the same (see FIGURE 1). However, habitat is unsuitable for use as a taxonomic basis because it is a character extrinsic to the plant.

The evidence provided above indicates that there are complex evolutionary relations among the taxa of the genus, and it is probably incorrect to divide these taxa into two groups. When we consider flower structure and fruit morphology, it appears that the genus should be accepted in its broad sense.

The systematic position of the genus has long been a subject of controversy. Rehder (1936) considered that the taxon did not seem to be closely related to any of the genera of the Tiliaceae or the Sterculiaceae. He thought that it was perhaps best placed in the Tiliaceae near *Luehea* Willd. because both lack androgynophores and have five bundles of stamens, although they differ markedly in flower sex, sepals, and fruits. Kostermans (1961) believed the genus to be most closely allied to *Colona* Cav. because both have a winged septicidal capsule. *Craigia* W. Smith & W. E. Evans, usually placed in the Sterculiaceae, was considered by Chang and Miau (1978) to be most closely related to *Burretiodendron* s.s. and *Excentrodendron* and had been included in their new subfam. Excentrodendroideae. In Hutchinson's (1967) system *Burretiodendron* was treated as one of the six genera under the tribe Enteleeae, based on the stamens all bearing fertile anthers and the fruits being capsules, but this is apparently not so.

The five-winged capsules of *Craigia* resemble the fruits of *Burretiodendron*. For this reason the two genera are often confused; for example *Craigia yunnanensis* has been misidentified as *B. combretoides* Chun & How (Chun & How, 1956) and *B. yunnanense* Kosterm. (Kostermans, 1961). *Craigia yunnanensis* can be most readily distinguished from *Burretiodendron* spp. by its petaloid staminodes and its lack of petals. I have examined the fruits of *Craigia yunnanensis* carefully. The species does have a loculicidal capsule rather than a septicidal one, which can be seen in the original drawing in Smith and Evans (1921). Evidence collected from palynology and wood anatomy also shows that the two groups have few similarities.

Burretiodendron differs from the other genera of tribe Enteleeae in having winged fruits that divide septicidally into five cocci. It differs markedly from *Colona* in having slender-clawed petals without a glandular portion at the base, and stamens connate into five bundles at the base.

So far the pollen morphology of over forty genera in the Tiliaceae has been studied by scanning electron microscopy. I have examined the pollen grains of several species of *Burretiodendron* under the SEM and have found three pollen patterns in this group: *B. hsienmu* with globular, panaperturate, coarsely reticulate grains (see FIGURE 2c); *B. esquirolii* with globular, panaperturate, papillate, echinate ones (see FIGURE 2b); and *B. kydiifolium* with oblate, monoporate, corrugate ones not previously recorded for the family (see FIGURE 2a). If palynology is considered, *Burretiodendron* seems to be more closely allied to *Schoutenia* Korth. and *Corchoropsis* Sieb. & Zucc. (see FIGURE 2). Morphologically it resembles *Schoutenia* and *Sicrea* Hallier f. in having an oblong, basifixed anther and two ovules in each locule and is much less similar to *Corchoropsis*. The latter is considered by many to be most closely related to

FIGURE 1. a–c, *B. esquirolii*: a, leaf; b, fruit; c, staminate flower. d–g, *B. kydiifolium*: d, leaf; e, fruit; f, carpellate flower; g, staminate flower. h, i, *B. hsienmu*: h, leaf; i, fruit. j, k, *B. obconicum*: j, leaf; k, fruit. l, *B. brilletii*, leaf. m, n, *B. siamense*: m, leaf; n, fruit.

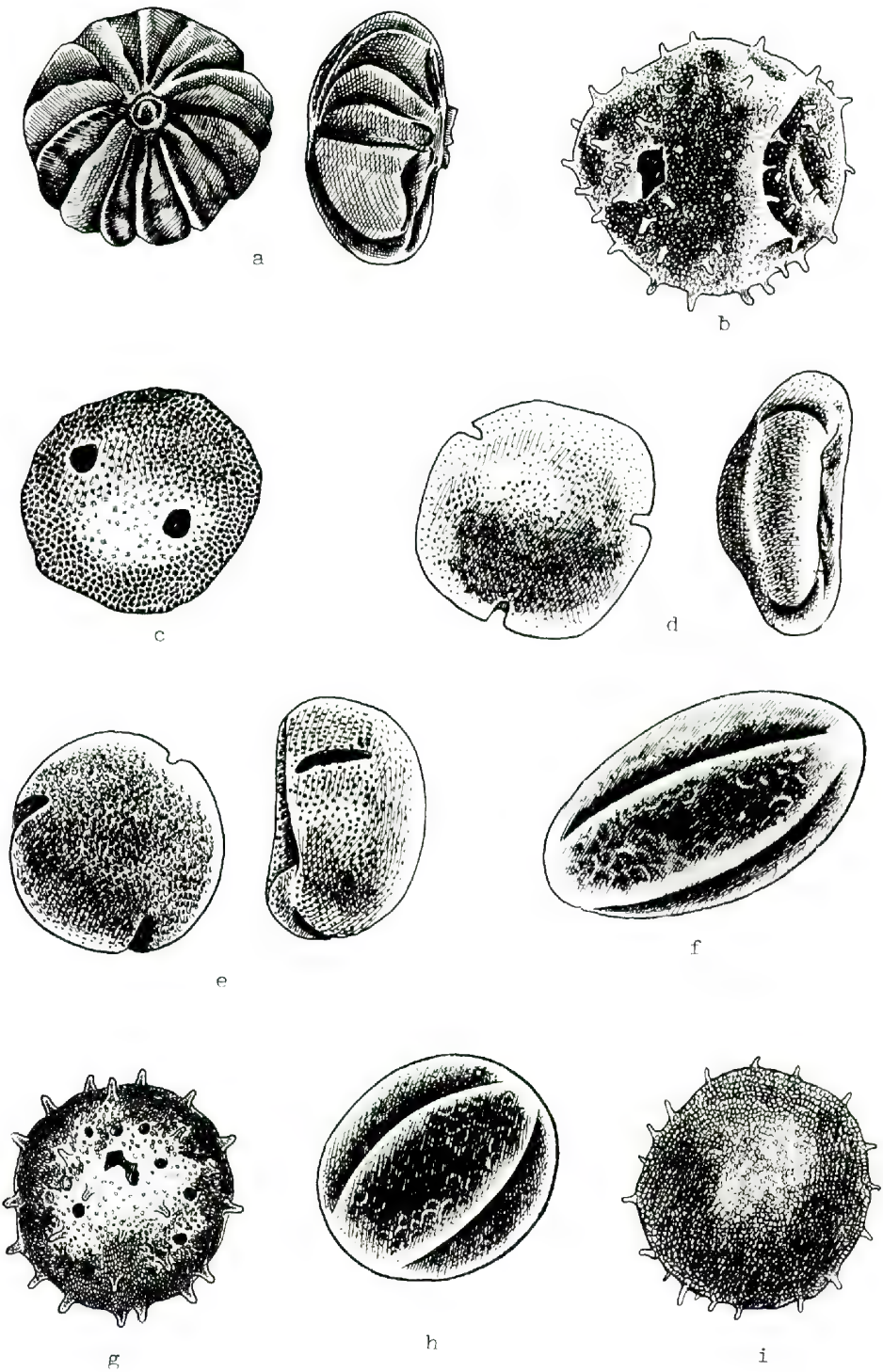

FIGURE 2. Pollen grains: a, *Burretiodendron kydiifolium*; b, *B. esquirolii*; c, *B. hsienmu*; d, *Tilia tuan* Szyszyl.; e, *Craigia yunnanensis* W. Smith & W. E. Evans; f, *Colona floribunda* Craib; g, *Corchoropsis crenata* Sieb. & Zucc.; h, *Luehea speciosa* Willd.; i, *Schoutenia ovata* Korth.

the Sterculiaceae. According to Erdtman's (1952) description, *Sicrea* is also similar to *Burretiodendron* in having globular, panaperturate pollen. The palynology hints that the systematic position of *Burretiodendron* may be near *Sicrea* and *Schoutenia*. Further studies will be necessary to resolve this question.

Five species of *Burretiodendron* have been reported from the border area between China and Vietnam. These exhibit almost all of the typical features of the group: for example, *B. kydiifolium* has the staminodes and the solitary carpellate flowers; *B. esquirolii*, the gynophore, the glandular sepals, and the two bracteoles enveloping a unisexual or bisexual flower bud; and *B. hsienmu*, the glands on the nerve axils and the three bracteoles enveloping a unisexual bud. Only one species, *B. siamense*, has a disjunct distribution, occurring in northern peninsular Thailand and the Mergui Archipelago of Burma. It therefore seems possible that *Burretiodendron* was derived in the border area between China and Vietnam.

Both *Burretiodendron hsienmu* and *B. kydiifolium* produce a very hard wood that can be used in building houses and boats. The most famous chopping blocks in the Kwangdong and Hong Kong regions are made of the "hsienmu" wood. Today the lumber resources of the genus are limited, and some species have been listed in the state catalogue of rare and endangered plants.

Burretiodendron Rehder, J. Arnold Arbor. **17:** 47. 1936. *Parapentace* Gagnep. Bull. Soc. Bot. France **90:** 70. 1943, *nomen nudum*. *Excentrodendron* H. T. Chang & R. H. Miau, Acta Sci. Nat. Univ. Sunyatsen **1978**(3): 21. 1978. TYPE SPECIES: *B. esquirolii* (Léveillé) Rehder.

Trees with leaves concentrated at ends of branchlets. Leaves alternate, simple; petiole usually long and slender, slightly swollen toward apex; stipules early caducous; blade palmati- or triplinerved, sometimes trilobate at apex, symmetrical or asymmetrical at base, entire. Flowers unisexual and sometimes bisexual (and plants polygamous), solitary or in small cymes, racemes, or panicles; bracteoles 2 or 3 enveloping flower bud, caducous; sepals 5, free, valvate, with or without glandular part inside at base; petals 5, free, more or less unguiculate. Staminate flowers with stamens numerous, connate at base into 5 phalanges; anthers basifixed, linear-oblong, bilocular, longitudinally dehiscent; staminodes absent or rarely present; ovary reduced. Carpellate and bisexual flowers with ovary 5-angular, 5-locular, 2-ovular in each locule; styles 5, free, clavate. Capsules 5-winged, splitting septicidally into 5 cocci. Seeds without endosperm; cotyledons large, foliaceous.

KEY TO THE SPECIES OF BURRETIODENDRON

A. Leaves with upper surface glabrous, margin entire but with apex sometimes 3-lobed; flowers unisexual, staminate ones in small panicles, carpellate ones solitary or in racemules; ovaries sessile.
  B. Leaves coriaceous or subcoriaceous, 3- to 5-basinerved; sepals usually glandular at base.
    C. Leaves oblong-elliptic or subrhomboid, acute or rotundate at base, 3-basinerved, nerve axils glandular.

D. Capsules 3–4 cm long, ellipsoid. ..... 1. *B. hsienmu.*
D. Capsules ca. 5 cm long, obconical. ..... 2. *B. obconicum.*
C. Leaves broadly ovate, subcordate or truncate at base, 5-basinerved, nerve axils eglandular. ..... 3. *B. brilletii.*
B. Leaves chartaceous, 5- to 9-basinerved; sepals eglandular at base.
E. Bracteoles 3; staminodes 5, linear; leaves cordate at base, 7- to 9-basinerved. ..... 4. *B. kydiifolium.*
E. Bracteoles 2; staminodes absent; leaves truncate or subcordate at base, 5- to 7-basinerved. ..... 5. *B. siamense.*
A. Leaves with both surfaces shortly stellate-pilose, margin denticulate; plants polygamous, flowers in cymes; ovaries stipitate. ..... 6. *B. esquirolii.*

1. **Burretiodendron hsienmu** W. Y. Chun & F. C. How, Acta Phytotax. Sin. **5:** 9. *t. 3.* 1956. *Excentrodendron hsienmu* (W. Y. Chun & F. C. How) H. T. Chang & R. H. Miau, Acta Sci. Nat. Univ. Sunyatsen **1978**(3): 23. 1978. TYPE: China, Kwangsi [Guangxi] Prov., Lungchow [Longzhou], Wu Lien Hsiang, April, 1955, *C. F. Liang 31523b* (holotype, SCBI!).
FIGURE 1h, i.

Pentace tonkinensis A. Chev. Bull. Econ. Indoch. **20:** 803. 1918, *nomen nudum*; Kostermans, Reinwardtia **5:** 239. 1960. *Parapentace tonkinensis* (A. Chev.) Gagnep. Bull. Soc. Bot. France **90:** 70. 1943. *Burretiodendron tonkinense* Kosterm. Reinwardtia **5:** 239. 1960. TYPE: Vietnam, Hoa-binh, *Brillet 8* (P; photo!).
Excentrodendron rhombifolium H. T. Chang & R. H. Miau, Acta Sci. Nat. Univ. Sunyatsen **1978**(3): 23. 1978. TYPE: China, Guangxi Prov., Longzhou, Qing-shan Xiang, *S. Q. Chen 11852* (holotype, SCIB!; isotype, IBG!).

Tree up to 40 m high. Leaves with petiole 4–10 cm long; blade orbicular-ovate to subrhomboid, 10–18 by 7–12 cm, long-acuminate at apex, acute or rotundate at base, coriaceous, glabrous, 3-basinerved, glandular in nerve axils. Flowers imperfect, staminate ones 6 to 12 in small panicles, carpellate ones solitary or 2 or 3 per racemule; bracteoles 3, caducous; sepals lanceolate, ca. 1–1.5 cm long, densely stellate-pilose, glandular inside at base; petals spathulate, clawed, about as long as sepals; stamens 25 to 35. Capsules ellipsoid, 3–4 cm long, glabrous.

DISTRIBUTION. China (Yunnan, Guangxi) and northern Vietnam.

ADDITIONAL SPECIMENS EXAMINED. **China.** YUNNAN PROV.: Hekou, *R. Zhuge 10276, 10277* (both SWFC), *C. J. Wang 1023* (SWFC); Jinping, *China–Soviet Union Exped. 1073* (KUN, PE); Malipo, *R. Zhuge 10274* (SWFC), *C. J. Wang 807* (SWFC). GUANGXI PROV.: Longzhou, *Y. K. Li 00243* (IBG, PE); Jinxi, *Z. M. Li & Z. J. Li 1368* (IBG); Ningming, *S. K. Lee 200409* (IBG); Baise, *Baise Exped. 01960* (PE); Debao, *Z. Y. Wei 00244* (IBG); Longan, *J. X. Zhong s.n.* 25 Feb. 1955 (SCBI). **Vietnam:** near Lao Cai, *China-Vietnam Exped. 717* (KUN).

Pentace tonkinensis, proposed by Chevalier in 1918, was briefly described in French. In 1943 the species was transferred by Gagnepain to his new genus *Parapentace,* which was merged by Kostermans in 1961 into *Burretiodendron*; there, Kostermans recognized it to be conspecific with *Burretiodendron hsienmu.* However, in 1978 Chang and Miau distinguished the species from *B. hsienmu* again, placing both in the new genus *Excentrodendron.* They believed

B. tonkinense to be characterized by fewer flowers in a raceme and a nodiferous pedicel, and *B. hsienmu* by numerous flowers in a panicle and an enodal pedicel. When I examined specimens of the two species in several larger Chinese herbaria, I found that the floriferous specimens were always identified as *B. hsienmu* and the fructiferous ones as *B. tonkinense*. Field observations revealed that staminate trees of *B. hsienmu* bear six to twelve flowers in small panicles, while carpellate trees have one to three flowers per raceme; the nodes on the pedicel are merely the cicatrices of the caducous bracteoles, as becomes apparent with the growth of the fruit. Furthermore, in Gagnepain's original description *Parapentace tonkinensis* was noted as "fl. ♂ groupées en glomérules de 10 environ." For this reason we can be sure that *B. tonkinense* only represents the carpellate trees of *B. hsienmu*. Although *B. hsienmu* was proposed later than *Parapentace tonkinensis*, it is considered to be the correct name of this species because *Parapentace* is an invalid name without Latin description or diagnosis.

Excentrodendron rhombifolium, reported from the same area as *Burretiodendron hsienmu*, was based on a single specimen with rhomboid leaves. Since I have collected similar leaves from trees of *B. hsienmu*, and the rhomboid leaf is only one of various leaf shapes characteristic of the species, it is better to reduce *E. rhombifolium* to synonymy under *B. hsienmu*.

2. **Burretiodendron obconicum** W. Y. Chun & F. C. How, Acta Phytotax. Sin. **5:** 11. *t. 4.* 1956. *Excentrodendron obconicum* (W. Y. Chun & F. C. How) H. T. Chang & R. H. Miau, Acta Sci. Nat. Univ. Sunyatsen **1978**(3): 24. 1978. TYPE: China, Guangxi Prov., Longzhou, Wu-lian Hsiang, July 1955, *C. F. Liang 31537* (holotype, SCBI!; isotype, IBG!). FIGURE 1j, k.

Tree 20 m tall. Leaves with petiole 4–8 cm long; blade elliptic to oblong-elliptic, 9–15 by 4.5–5.5 cm, long-acuminate at apex, acute at base, subcoriaceous, glabrous, 3-basinerved, nerve axils glandular. Flowers unknown. Infructescences racemose or dichotomous. Capsules obconical, ca. 5 cm long, glabrous.

DISTRIBUTION. China (Guangxi).

Burretiodendron obconicum is very similar to *B. hsienmu* in having three-basinerved, glandular, coriaceous leaves but differs in having obconical capsules and oblong-elliptic leaves. It is confined to southern Guangxi Province close to the border of China and Vietnam.

3. **Burretiodendron brilletii** Kosterm. Reinwardtia **5:** 240. 1960. *Parapentace brilletii* Gagnep. Bull. Soc. Bot. France **90:** 71. 1943. TYPE: Vietnam, Hoa-binh, *Brillet 19* (holotype, P; isotype, BO). FIGURE 1l.

Tree; branchlets densely and minutely gray-stellate-tomentose. Leaves with petiole slender, 1.5–4 cm long, densely minutely stellate-pilose; blade broadly ovate to suborbicular, 7–11 by 4–10 cm, acuminate at apex, subcordate or truncate at base, subcoriaceous, both surfaces densely reticulate, 5-basinerved, nerve axils eglandular but with scattered stellate hairs present on nerves below. Inflorescences axillary fascicles. Staminate flowers in lax panicles; sepals lan-

ceolate, glabrous inside with small nectariferous basal part; petals spathulate, slightly longer than sepals; stamens 15 to 18; pistillode ovoid, 1 mm in diameter, stellate-pilose, apex tricuspidate. Carpellate flowers and fruits unknown.

DISTRIBUTION. Northern Vietnam.

ADDITIONAL SPECIMEN EXAMINED. **Vietnam:** Tudin, *Nghien s.n.* 29 Jan. 1961 (KUN).

Burretiodendron brilletii, first reported by Gagnepain in 1943 under *Parapentace* (based on a specimen bearing staminate flowers), is still poorly known. It is rare and confined to northern Vietnam. It differs from the other species of *Burretiodendron* in having broadly ovate to suborbicular, five-basinerved leaves with the base subcordate and the nerve axils eglandular.

4. **Burretiodendron kydiifolium** Hsu & Zhuge, sp. nov. FIGURE 1d–g.

Haec species a speciebus ceteris generis bene distincta; differt a *B. esquirolii* Rehder foliis glabris, bracteolis 3, floribus ♂ staminodiis 5, linearibus, ovariis sessilibus, a *B. hsienmu* foliis crasso-chartaceis, basi late cordatis, 7–9 palminervatis.

Tree up to 15 m high; branchlets densely brown-stellate-lepidote. Leaves with petiole 3.5–10 cm long, glabrous; blade chartaceous, suborbicular, 7–15 by 7–13 cm, sometimes 3-lobed at apex, cordate at base, entire, 7- to 9-basinerved. Staminate flowers 3 to 7 per raceme, carpellate ones solitary or rarely 2 or 3 per raceme; bracteoles 3 enveloping flower bud; sepals oblong-elliptic, 6–8 cm long, not glandular inside near base; petals flabelliform, apex praemorse, base cuneate; stamens 25 to 30; staminodes 5, linear, longer than stamens; ovary 5-angular with 5 free clavate styles. Capsule ellipsoid, 3–4 cm long.

TYPE. China, Yunnan Prov., valley of Yuanjiang River, 480 m alt., 12 May 1986, *R. Zhuge 10418* (holotype, SWFC; isotype, KUN).

DISTRIBUTION. Known only from Yunnan, China.

ADDITIONAL SPECIMENS EXAMINED. **China.** YUNNAN PROV.: valley of Yuanjiang R., 820 m alt., *R. Zhuge 90669, 90670* (both SWFC).

Burretiodendron kydiifolium corresponds to a set of flowering and fruiting specimens that I collected from the valley of the Yuanjiang River in Yunnan Province. It resembles *B. siamense* somewhat in having chartaceous, broadly ovate, five-basinerved leaves that are often three-lobed at the apex, but the two species are quite distinct. The flowers of *B. kydiifolium* have three (vs. two) bracteoles and five staminodes.

5. **Burretiodendron siamense** Kosterm. Reinwardtia **6:** 4. *t. 2.* 1961. TYPE: northern peninsular Siam, Khao Chawng Kachok, common in deciduous forest, *Thaew Sinthiphongse 27* (holotype, BKF). FIGURE 1m, n.

Burretiodendron esquirolii auct. non Rehder: Smitin. Nat. Hist. Soc. Bull. Siam **19:** 88. 1958.

Tree 8–12 m tall; branchlets densely very shortly brown-stellate-lepidote-pilose. Leaves with petiole up to 5 cm long, glabrous; blade broadly ovate, 8–15 by 5.5–10 cm, sometimes 3-lobed at apex, truncate or subcordate at base, entire, chartaceous, 5- to 7-basi-nerved, glabrescent. Flowers solitary, subtended by 2 large, broadly ovate bracteoles; sepals lanceolate-ovate; petals broadly elliptic, slightly longer than sepals, membranous; stamens numerous. Capsules oblong-ellipsoid, 5–6 cm long, glabrous.

DISTRIBUTION. Northern peninsular Thailand, Mergui Archipelago of Burma.

Kostermans' (1961) original description of *Burretiodendron siamense* was based on fruiting specimens collected from northern peninsular Thailand and the Mergui region of Burma. The description of the flowers was added in 1965. This species can be readily distinguished from the others in the genus by its solitary flower with two bracteoles and its much bigger fruits.

6. **Burretiodendron esquirolii** (Lévl.) Rehder, J. Arnold Arbor. **17:** 48. *t. 178.* 1936. *Pentace esquirolii* Léveillé, Repert. Sp. Nov. **10:** 147. 1911. TYPE: China, Kweichow [Guizhou] Prov., west of Lo-fou, Nov. 1905, *J. Cavalerie 2648* (holotype, E; photo and fragment of holotype, A).

FIGURE 1a–c.

Eriolaena esquirolii Léveillé, Fl. Kouy-Tchéou, 405. 1916. TYPE: China, Kweichow [Guizhou], Yang-ly, Aug. 1911, *J. Esquirol 2717* (holotype, E; photo and fragment of holotype, A).

Burretiodendron longistipitatum R. H. Miau, Acta Sci. Nat. Univ. Sunyatsen **1978**(3): 25. 1978. TYPE: China, Guangxi Prov., Long-lin, 26 Oct. 1957, *C. C. Chang 4755* (holotype, IBG!).

Tree up to 20 m high; branchlets densely minutely stellate-pilose. Leaves with petiole 3–9 cm long, slender, densely stellate-pilose; blade ovate to subrotundate, 10–25 by 8–20 cm, acute at apex and often 3-lobed, cordate at base, denticulate, chartaceous, palmately 5- to 7-nerved, both surfaces densely stellate-pilose. Plants polygamous, flowers 3 to 11 in small cymes; bracteoles 2, caducous, broadly ovate to elliptic; sepals ovate-elliptic, glabrous inside with 1 or 2 basal, oblong, elevated, glandular areas; petals broadly obovate, slightly longer than sepals, margin ciliolate; stamens ca. 30; ovary ovoid, 5-angular, with 5 clavate styles and gynophore. Capsules oblong in outline, 4–5 cm long.

DISTRIBUTION. China (southeastern Yunnan, southern Guizhou, and Guangxi provinces).

ADDITIONAL SPECIMENS EXAMINED. **China.** YUNNAN PROV.: Yuanjiang, *R. Zhuge 90607, 90608* (both SWFC), *G. D. Tao 38162, 38164* (both YTBG); Shibing, *Yunnan Forestry Institute 77153* (YNFI); Jinping, *China–Soviet Union Exped. 2617, 2618* (both KUN). GUIZHOU PROV.: Ceheng, *Z. Y. Chao 1208* (KUN, PE); Luodian, *Z. J. Luo 2661, 3667* (both GZFI); Wengan, *Li-po Exped. 1930* (GZFI). GUANGXI PROV.: Longlin, *C. C. Chang 10236* (IBG, SCBI); Tiane, *Z. T. Li 601284* (IBG).

The first species of *Burretiodendron,* originally described as *Pentace esquirolii,* was based on three specimens collected by J. Cavalerie and J. Esquirol at Lofou and Yangli, Guizhou Province, China. *Cavalerie 2648* was the holotype of the

species. *Esquirol 817* and *2717* were both cited in *Flore du Kouy-Tchéou* (Léveillé, 1915) under *P. esquirolii,* and the latter again under *Eriolaena esquirolii.* They were all recognized by A. Rehder (1936) to be different from *Pentace* and other genera of the Tiliaceae in having unisexual flowers, five-winged fruits dehiscing into free cocci, and sepals with glands. Within *Burretiodendron, B. esquirolii* is easily distinguished from the other species by its pubescence and its longer fruit pedicels.

Burretiodendron longistipitatum was based on a single specimen with fruit pedicels a little longer than those of *B. esquirolii.* This is quite a variable character, and the same variability is also found in specimens of *B. esquirolii.* This species is therefore reduced to synonymy under *B. esquirolii.*

EXCLUDED SPECIES

Burretiodendron umbellatum Kosterm., which was reported in 1962 from Thailand, was regarded as a doubtful species by Chang and Miau in 1978. As early as 1965 Kostermans, relying on additional and better materials from the same location, had revealed that the species was identical with *Mansonia gagei* Prain (Sterculiaceae).

ACKNOWLEDGMENTS

I would like to thank my advisers, professors Hsu Yung-chun (Southwest Forestry College, Kunming, China) and Chen Cheih (Kunming Botanical Institute, Academia Sinica) for comments and criticisms on the contents of this paper; Dr. J. E. Vidal (Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris) for kindly sending photographs of specimens; and Mr. Li Nang (Southwest Forestry College, Kunming) for the artwork.

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DESMODIUM SCHUBERTIAE (LEGUMINOSAE), A NEW SPECIES FROM CAMBODIA AND VIETNAM

Hiroyoshi Ohashi[1]

A new species of *Desmodium* (Leguminosae-Papilionoideae), *D. schubertiae* Ohashi, is found in Cambodia and Vietnam. It resembles *D. rubrum* (Lour.) DC. and is thought to have evolved from *D. heterocarpon* (L.) DC.

While preparing a treatment of *Desmodium* Desv. for the *Flore du Cambodge, du Laos et du Vietnam* at the Harvard University Herbaria in 1988, I found a new species of *Desmodium* among the specimens collected by Poilane in Cambodia and Vietnam and kept in the herbarium of the Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle (P). It is named in honor of Dr. Bernice G. Schubert, of the Arnold Arboretum of Harvard University, in recognition of her distinguished contribution to taxonomic research in *Desmodium*. In the present paper, the new species is described and its taxonomic relationships are discussed.

Desmodium schubertiae Ohashi, sp. nov. FIGURE.

Species haec a Desmodio rubro differt foliolis inferioribus dense sericeis, anguste ellipticis vel oblongo-ellipticis; calycibus lobis adaxialibus apicis profunde bifidis; ovariis uncinulato- et glandulifero-puberulis; leguminibus ad suturas inferiores uncinulato-puberulis, cetero glabrescentes, ad suturas superiores incrassatis.

TYPE: Vietnam (Annam), Prov. du Darlac, massif du Chu Yang Siuh, 1500 à 1800 m alt., sol granitique médiocre, 22 April 1941, *E. Poilane 32489* (holotype, P; isotype, TUS; photo of holotype, A).

Shrubs ca. 2 m high, freely branched; young branches densely covered with appressed, silky, white or ferrugineous hairs and spreading, minute, hooked hairs. Leaves 1-foliolate; stipules persistent even on 2- to 4-year-old branches, free, narrowly long-triangular with filiform apex, 7–9 mm long, ca. 1 mm wide at base, ciliate, scarious, striate, glabrous inside, densely appressed-pubescent outside; petiole 8–15 mm long, densely strigose with appressed, ferrugineous hairs. Leaflets narrowly elliptic or oblong-elliptic, 2–4 cm long, 8–18 mm wide, obtuse to emarginate at apex, obtuse or rounded at base, entire and densely ciliate, subcoriaceous, the upper surface thinly pubescent with appressed soft hairs ca. 0.5 mm long, the lower surface densely so with ascending silky hairs

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Journal of the Arnold Arboretum **71**: 381–384. July, 1990.

Desmodium schubertiae: a, holotype; b, pods, ×2.

to 1.5 mm long, the principal lateral nerves 6 to 8 on each side of midrib, prominent and not directly reaching margin, the cancellate veins inconspicuous below; stipels subulate, 4–5 mm long, silky outside. Inflorescences terminal and occasionally axillary, pseudoracemose, 7–14 cm long, 2-flowered at each node; rachis with dense spreading, hooked hairs ca. 0.3 mm long. Pedicels 5–6 mm long, spreading–hairy with straight, rigid hairs less than 0.5 mm long, glandular hairs ca. 0.3 mm long, and minute, hooked hairs ca. 0.1 mm long. Primary bracts ovate with acuminate apex, 6–7 mm long, 2–2.5 mm wide, scarious, striate, glabrous inside, with dense minute, hooked hairs and dense subspreading, straight hairs outside; secondary bracts and bracteoles absent. Calyces 3.5–4 mm long, pubescent with straight hairs and minute hooked hairs, 4-lobed, lobes longer than tube, the upper one 2.5–3 mm long, bifid at apex, teeth ca. 1 mm long, the lateral ones narrowly triangular, the lowest one longest. Flowers ca. 6 mm long, violet-rose; androecium diadelphous, the filaments glabrous; ovary and lower part of style covered with minute hooked hairs and glandular hairs. Pods ascending, sessile, narrowly oblong, 1.5–2.5 cm long, ca. 4 mm wide, straight, with 3 to 5 articles, dehiscent along lower suture, this undulate, with minute thinly uncinate hairs, the upper suture almost straight, much thickened, glabrescent, the lateral surfaces with prominent reticulate veins, glabrescent; articles 4.5–5 mm long. Seeds compressed-reniform, ca. 3.5 mm long, 2.5 mm wide, reddish purple, rim-arillate around hilum.

ADDITIONAL SPECIMENS EXAMINED. **Cambodia:** Bokor, montagnes de l'Éléphant, 1000 m alt., *E. Poilane 23059* (P, TUS; photo A).

Desmodium schubertiae belongs to sect. *Nicolsonia* of subg. *Sagotia* because its pods, calyces, and bracts agree with those characterized for this section. It is a group of 12 Asiatic species (Ohashi, 1973). Of these, *D. ferrugineum* Wallich ex Thwaites, *D. heterocarpon* (L.) DC., *D. jucundum* Thwaites, *D. nemorosum* F. Mueller ex Bentham, and *D. rubrum* (Lour.) DC. are similar to the new species in general appearance. These six species can be distinguished from each other by the following key:

1. Articles of pod at least twice as long as broad. ..... *D. nemorosum.*
1. Articles of pod less than twice as long as broad.
   2. Leaves 3- or (1- to) 3-foliolate.
      3. Pods stalked, reflexed when mature. ..... *D. ferrugineum.*
      3. Pods sessile, erect or ascending when mature.
         4. Leaflets coriaceous, with lateral nerves elevated below; leaves 3-foliolate; stipules broadly ovate, 5–6 mm wide; articles 5–6 mm long. ..... *D. jucundum.*
         4. Leaflets not as above; leaves 1- and 3- or all 3-foliolate; stipules narrowly triangular, less than 3 mm wide; articles less than 4.5 mm long. ..... *D. heterocarpon.*
   2. Leaves 1-foliolate.
      5. Leaflets glabrescent below, elliptic to nearly orbicular, with 4 to 6 pairs of lateral nerves; upper calyx-lobes minutely bifid at apex; ovary glabrous; pods glabrous, with upper suture only slightly thickened. ..... *D. rubrum.*
      5. Leaflets densely silky-hairy below, narrowly elliptic or oblong-elliptic, with 6 to 8 pairs of lateral nerves; upper calyx-lobes distinctly bifid at apex; ovary

with minute hooked hairs and glandular hairs; pods glabrescent except on lower suture, with upper suture much-thickened. ..... *D. schubertiae.*

Although *Desmodium schubertiae* is most similar to *D. rubrum* in the characters indicated in the foregoing key, it is most closely related to *D. heterocarpon.* There are fundamental similarities among these three species in habit, leaflets, flowers, and pods. However, *D. schubertiae* is found in mountainous regions between 1000 and 1800 m elevation, while *D. rubrum* is found at the seaside or in open places at low altitudes. There is a significant difference in distribution between these two species. *Desmodium heterocarpon* occurs in the tropical, subtropical, and warm regions of India, southeastern and eastern Asia, the Pacific islands, and Australia. It is common on sunny roadsides through forests, in thickets, or in grasslands, from sea level to more than 1000 m altitude, and is possibly sympatric with both *D. schubertiae* and *D. rubrum* in Indochina.

In Indochina and neighboring regions are concentrated *Desmodium harmsii* Schindler (southern Vietnam), *D. rubrum* (Vietnam; Hainan and Kwangtung, People's Republic of China), *D. schubertiae* (Vietnam, Cambodia), and *D. strigillosum* Schindler (Burma (rare), Laos, Cambodia, and Vietnam), all endemic species of sect. *Nicolsonia.* This distribution pattern is a characteristic feature of the section. Moreover, *D. griffithianum,* which occurs in India (Assam), Burma, Thailand, Laos, Vietnam, and southwestern China, and *D. toppinii,* endemic to Burma, show related patterns of distribution. All these species are considered to be most closely related to *D. heterocarpon* (Ohashi, 1973) and perhaps are derived from it.

Desmodium schubertiae is therefore thought to be derived from *D. heterocarpon* in a mountainous region of Cambodia and Vietnam, and *D. rubrum* may also be evolved from *D. heterocarpon,* having adapted to open places near the sea or at low elevations.

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A NOTE ON THE CHILEAN ENDEMIC DRABA THLASPIFORMIS (BRASSICACEAE)

Ihsan A. Al-Shehbaz[1]

A new combination based on *Eudema thlaspiforme* is proposed in *Draba*. The species is described and illustrated.

Draba thlaspiformis (Philippi) Al-Shehbaz was originally described by Philippi (1872) as a questionable species of *Eudema* Humb. & Bonpl. Gilg and Muschler (1909) transferred it to *Lesquerella* S. Watson but gave no justification for that transfer. Schulz (1924) maintained it in the latter genus and later (Schulz, 1929) gave it a new name, *Draba philippii* O. E. Schulz, which he based on a type different from that of *E. thlaspiforme* Philippi. The species is a perfectly good representative of *Draba* and has nothing to do with either *Eudema* or *Lesquerella*. Philippi's name is the earliest legitimate name for the species, and there are no nomenclatural obstacles preventing its transfer to *Draba*. Therefore, a new combination based on *E. thlaspiforme* is needed in *Draba*. A detailed description and an illustration are provided below in order to assist in the determination of this very rare and obscure species.

Draba thlaspiformis (Philippi) Al-Shehbaz, comb. nov. FIGURE.

Eudema thlaspiforme Philippi, Anal. Univ. Santiago **41:** 675. 1872. *Lesquerella thlaspiformis* (Philippi) Gilg & Muschler, Bot. Jahrb. Syst. **42:** 466. 1909. TYPE: Chile, [Región Metropolitana de Santiago,] valle de Maipo, mina Cristo, *Dávila s.n.*, 1870 (holotype, SGO; isotypes, B!, GH!).

Draba philippii O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem **10:** 599. 1929. TYPE: Chile, [Región Metropolitana de Santiago,] Cordillera de Maipú, *Philippi s.n.* (holotype, B!).

Perennial herbs. Trichomes short stalked, stellate, to 0.3 mm in diameter; rays basically 4, 1 to all furcate or trifid at variable distances from stalk, very rarely all unbranched. Stems several from base, ascending, 7–12 cm tall, sparsely pubescent. Basal leaves rosulate, short petiolate, oblong, obtuse; cauline leaves sessile, oblong to oblong-elliptic, 10–15 mm long, 4–6 mm wide, entire, sparsely pubescent. Inflorescences corymbose racemes, elongated in fruit, lowermost flowers bracteate. Sepals erect, somewhat persistent, broadly oblong, 2.5–3 mm long, 1.5–2 mm wide, sparsely pubescent, rounded at apex, membranaceous margin to ca. 0.4 mm wide. Petals clawed, broadly obovate, 6–7 mm long, 2.5–3 mm wide, white. Filaments erect, conspicuously dilated at

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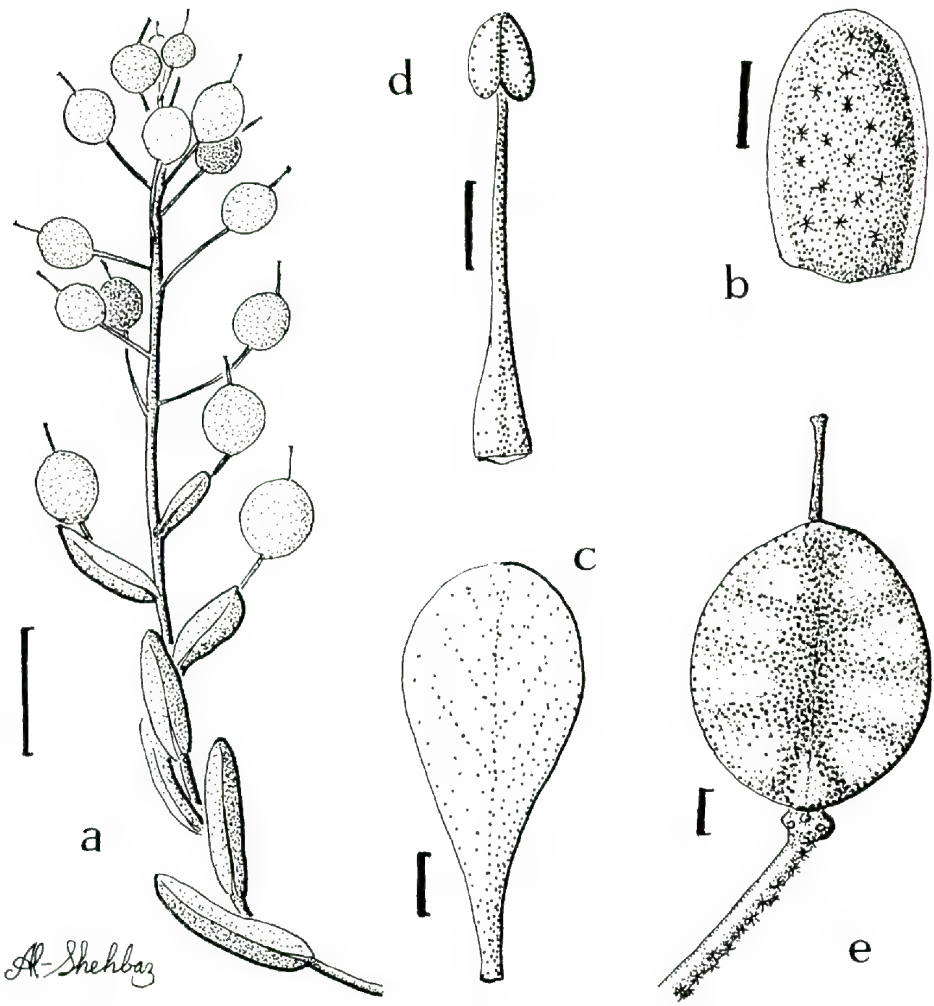
Journal of the Arnold Arboretum **71:** 385–387. July, 1990.



Draba thlaspiformis (from *Philippi s.n.*): a, infructescence and portion of stem; b, sepal; c, petal; d, stamen; e, fruit. Scale bars = 1 cm (a), 1 mm (b–e).

base, 3–4.5 mm long, white; anthers ovate, 0.6–0.8 mm long. Nectar glands 4, 1 on each side of lateral stamen, low. Fruiting pedicels divaricate, straight, (3–)5–10(–15) mm long, glabrous on upper surface, sparsely pubescent on lower. Fruits sessile, suborbicular, strongly flattened parallel to septum, 5–8 mm long, 4–6 mm wide; valves thin, rounded at apex and base, glabrous, obscurely nerved; septa complete; style slender, 2–3 mm long, glabrous; stigma slightly 2-lobed. Mature seeds not seen.

Draba thlaspiformis is apparently known only from the two type collections that were made some 120 years ago. It is closely related to *D. gilliesii* W. J. Hooker & Arn., from which it is easily distinguished in having untwisted, suborbicular fruits and bracteate lower portions of inflorescences, as well as

lacking median nectaries. In contrast, *D. gilliesii* has oblong to lanceolate or linear, usually twisted fruits, ebracteate inflorescences, and median nectaries that subtend the bases of paired filaments.

ACKNOWLEDGMENTS

I am grateful to Oanh Tran for typing the manuscript and to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice.

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BOOK REVIEW

Trees, Shrubs, and Woody Vines of Northern Florida and Adjacent Georgia and Alabama, by Robert K. Godfrey, with the majority of illustrations by Melanie Darst. University of Georgia Press, Athens and London, 1989. ix + 734 pp. ISBN 0-8203-1035-2. $50 hardcover.

As might be expected from his previous splendid publications and his extraordinary field knowledge, Robert Godfrey's new book on the woody plants of northern Florida and adjacent areas is a superb addition to the botanical literature of the Southeast. Having done extensive field work myself in the area many years ago, I perused this book very carefully to see which of my woody species he had omitted and which I might have overlooked in southwestern Georgia. Of the former, *Corylus americana* Walter and *Crataegus brachyacantha* Englem. & Sarg. apparently have not been found in northern Florida. *Agave virginica* L. and *Erythrina herbacea* L. surely have been found there but arguably lack sufficient woodiness in northern Florida to qualify for the book, although in peninsular Florida *E. herbacea* does become a sizable shrub or small tree. I had failed to find, or at least to recognize, perhaps ten species attributed by Godfrey to southwestern Georgia. In 1946–1949 most of them were not generally recognized as distinct species or were not known from southern Georgia. I should like to look for them there now. I was particularly delighted to note that *Bumelia thornei* Cronq., of the Sapotaceae, has not only been rediscovered in Georgia but has been added by Godfrey to the Florida flora.

Godfrey's taxonomy is rather traditional. His species and generic concepts and nomenclature are most acceptable and up to date, but his disinterest in phylogeny is apparent. *Nandina* is still retained in the Berberidaceae, *Sambucus* and *Viburnum* in the Caprifoliaceae, *Phoradendron* in the Loranthaceae, *Nyssa* in the Nyssaceae, and *Decumaria, Hydrangea, Itea, Philadelphus,* and *Ribes* in the Saxifragaceae. On the other hand, the family name Avicenniaceae is accepted for *Avicennia,* the Black Mangrove. For ready reference the families are arranged alphabetically in the major groups, but unfortunately four of the larger families must be sought under the older names Gramineae, Palmae, Guttiferae, and Leguminosae. I should have preferred that species, like genera, be consistently arranged in alphabetical order.

The category "subspecies" should have been employed more frequently. I have long believed that use of that category would solve some of the most difficult taxonomic problems among southeastern woody plants—for example, in such closely related pairs as *Juniperus virginiana–J. silicicola, Taxodium distichum–T. ascendens, Myrica cerifera–M. pusilla, Nyssa sylvatica–N. biflora, Toxicodendron radicans–T. toxicarium, Cyrilla racemiflora–C. parvifolia, Tilia*

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Journal of the Arnold Arboretum **71:** 389, 390. July, 1990.

americana–T. heterophylla, Clethra alnifolia–C. tomentosa, Halesia diptera var. *diptera* and var. *magniflora,* and probably many more. The subspecific treatment of the southern sugar maples is a good example of what can thereby be achieved.

The original descriptions and keys are accurate, thorough, well done, and reflective of the author's field acumen. The keys particularly are readily usable for identification and for differentiation of taxa because of the emphasis on vegetative characteristics. Excellent full-page drawings are supplied for almost all species, both indigenous and naturalized, and add much to the value of the book. Statements on habitats and distribution again reflect the broad field knowledge of the author and his careful study of floristic literature.

A useful glossary follows the introduction. Several pages of pertinent references precede the indexes to common and scientific names (I would have preferred that the two indexes be combined). Proofreading must have been painstaking, for I found very few errors. On page 132 *A. incanna* and on page 133 *A. incarna* are used for *Asimina incana* (Bartram) Exell. Apparently Godfrey prefers to use Bartram's original misprint *A. incarna* for this species, despite Exell's selection of *A. incana* as the intended correct name. Job Kuijt might be surprised at the misspelling of his name on page 454.

This book is a "must" addition to the bookshelf for anyone interested in identification of woody plants of the American Southeast or in the southeastern flora and woody plants, ecology, and phytogeography in general. As book prices go nowadays, $50 is reasonable for such an informative, well-illustrated, well-printed, and well-bound tome.—Robert F. Thorne, Rancho Santa Ana Botanic Garden, Claremont, California 91711.

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JOURNAL OF THE ARNOLD ARBORETUM

HARVARD UNIVERSITY VOLUME 71 NUMBER 4

ISSN 0004–2625

Journal of the Arnold Arboretum

The *Journal of the Arnold Arboretum* (ISSN 0004-2625) is published quarterly in January, April, July, and October for $70.00 per year, plus $10.00 or $15.00 postage for addresses outside of the United States, by the Arnold Arboretum of Harvard University. It is printed and distributed by Allen Press, Inc., 1041 New Hampshire Street, Lawrence, Kansas 66044. Second-class postage paid at Lawrence, Kansas. POSTMASTER: send address changes to *Journal of the Arnold Arboretum,* % Allen Press, Inc., P.O. Box 368, Lawrence, Kansas 66044.

Because publication of the *Journal of the Arnold Arboretum* is being suspended after Volume 71 (1990) has been completed, subscriptions can only be accepted for the present volume. Remittances for Volume 71 should be sent to *Journal of the Arnold Arboretum,* 1041 New Hampshire Street, Lawrence, Kansas 66044, U.S.A. Claims will not be accepted after six months from the date of issue.

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COVER: The stylized design appearing on the Journal and the offprints was drawn by Karen Stoutsenberger.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME 71 OCTOBER 1990 NUMBER 4

THE GENERA OF CARDUEAE (COMPOSITAE; ASTERACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

RANDALL W. SCOTT[2]

Tribe **Cardueae** Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88:** 155. 1819, "Carduineae."

Perennial to annual herbs [rarely shrubby or tree-like]. Leaves alternate, sinuate, lobed, pinnatifid or pinnatisect, rarely entire, commonly spiny margined. Capitula (heads) homogamous or heterogamous with carpellate or neuter (sterile) and partly radiating marginal flowers. Involucral bracts ovate to lanceolate [bristles], imbricate in several series, often with an apical spine, bristle, or membranaceous appendage. Receptacle setaceous, bristly, hairy or honeycombed [naked or with connate bracts partially split at the upper margin].

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8415769 (Carroll E. Wood, Jr., principal investigator), under which this account was prepared, and BSR-8415637 (Norton G. Miller, principal investigator). This treatment, the 134th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family, subfamily, tribe, subtribe, or genus in brackets [ ]. Those references that I have not verified are marked with an asterisk.

I want to thank Carroll Wood for his extensive and constructive comments, both editorial and otherwise. Particular thanks go to Tina Ayers without whose support this project might never have been completed. Ihsan Al-Shehbaz and Barbara Callahan were very helpful with bibliographic searches, while I was at Harvard. For assistance manifested in a variety of ways, I want to thank David Boufford, Barbara Nimblett, Cathy Paris, John Pruski, Stephen Spongberg, and Emily Wood.

The illustration was drawn under an earlier NSF grant by Rachel A. Wheeler supervised by George K. Brizicky from materials collected by C. E. Wood, Jr. (a–e, j) and J. K. Small (*8122,* GH) in Florida, and by R. B. Channell and H. F. L. Rock in southeastern North Carolina.

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Journal of the Arnold Arboretum **71:** 391–451. October, 1990.

Pappus of simple or plumose bristles or paleaceous, uniseriate (*Echinops*) or multiseriate, free or basally fused, of nearly equal length (Carduinae), or the inner longer (Centaureinae). Corollas tubular (*Echinops*), actinomorphic, divided into tube and limb, the outer florets occasionally zygomorphic (falsely radiate) (*Cirsium, Centaurea*), lobes narrow or linear [triangular] and, in many cases, elongated. Anthers with sagittate basal appendages, these entire or denticulate [laciniate]; filaments hairy, papillose or glabrous; pollen variable, but basic type spherical, spiny, tricolporate (see Wagenitz, 1955; Štepa). Styles very long, united and only diverging at the tips (see Solbrig, 1963, *fig. 2, l*) or widely divergent or very short and divergent, often with a distinct collar of hairs at or below the base of the flat, elliptical or semi-cylindrical, acute to acuminate, often papillose branches, the stigmatic papillae on the inner surface. Achenes mostly obovate, elongate-conoidal or fusiform, commonly somewhat bossed on the upper, abaxial side, occasionally laterally compressed, glabrous or sparsely covered with one-celled hairs or shortly forked twin hairs to densely villous (*Echinops*); often with a distinctly marked apical crown or margin; detachment area of achenes straight and basal (*Echinops*), straight and lateral-adaxially, lateral-abaxially, rarely basally oriented (Carduinae) or concave and lateral-adaxially oriented (Centaureinae); seed often with a basal or lateral (*Centaurea* and related genera) hilum. (Carlineae Cass., Jour. Phys. **88:** 152. 1819; Centaurieae Cass., *Ibid.* 154; Echinopseae Cass., *Ibid.* 157; Cynareae Less., Linnaea **5:** 128. 1830, nom. illegit. [includes *Carduus* L., type of Cardueae Cass.].) TYPE GENUS: *Carduus* L.

Nearly 80 genera (ca. 2500 spp.; Dittrich, 1977) traditionally placed in four subtribes, but more recently (Dittrich, 1977) segregated into three tribes: Echinopseae Cass., Carlineae Cass., Cardueae Cass., with the last divided into subtribes Carduinae Dumort. and Centaureinae Dumort. Genera known from the Southeast belong to the Cardueae (Dittrich, 1977). *Arctium* L., *Carduus* L., *Cirsium* Miller, *Onopordum* L., and *Silybum* Adanson were placed in the Carduinae and *Centaurea* L. and *Cnicus* L. in the Centaureinae. The Echinopseae Cass. may be represented in the Southeast by *Echinops* L., but there is no solid evidence that any of the cultivated species has escaped from cultivation there. Centers of diversity are in Europe and western Asia. About 35 species in eight genera occur in the southeastern United States. The great majority of the North American representatives of this tribe have been introduced from Europe. Native taxa from the Southeast occur only in *Cirsium* (all but two of the nearly fifteen species are indigenous) and *Centaurea* (one of eight species is native).

Considerable diversity of opinion has been expressed in the nomenclatural history of the Cardueae. In a serial treatment that extended over a period of nearly fifteen years, Cassini (1816–1830) described numerous taxa in the tribes Cardueae Cass., Centaurieae Cass., Carlineae Cass., and Echinopseae Cass. These tribes were first described under their French names (Cassini, 1817), but were later given Latin names by Cassini (1819). Two years after Cassini finished his serial treatment, Lessing presented a more inclusive treatment of the family wherein he placed most of six of Cassini's tribes under the illegitimate name Cynareae Less. Bentham (1873a, b) included four of Cassini's tribes in the

Cardueae ["Cynaroideae"] in what came to be the traditionally accepted view of the tribe. Most recently, Dittrich (1977) recognized three tribes in lieu of Bentham's single broadly circumscribed one.

As indicated by Dittrich (1977), the superfluous name Cynareae, coined by Lessing, has been used by many authors (e.g., Boissier; Bentham; Hoffmann) and still persists in contemporary works (e.g., Carlquist, 1965; Cronquist, 1955, 1977; Dittrich *et al.*, 1979, 1980; Clapham *et al.*; Jeffrey, 1968; Johnson 1974, 1975).

The following genera known from the southeastern United States were included in Cassini's Cardueae: *Arctium* (as *Lappa* Scop.), *Carduus, Cirsium, Onopordum,* and *Silybum.* He placed *Cnicus* and *Centaurea* in the Centaurieae. Several taxa treated by Cassini as subtribe Xeranthemées of the tribe Carlineae have been placed in the Cardueae by subsequent workers.

In a treatment published a year before Cassini finished his extended serial treatment of the Compositae, Dumortier retained the tribes Echinopseae (as Echinopsideae) and Cardueae (as Carduaceae), but reduced Cassini's tribes Carlineae and Centaurieae to subtribes of the Cardueae.

Lessing incorporated all or parts of five of Cassini's tribes (Arctotideae, Calenduleae, Cardueae, Centaurieae, Echinopseae) and the subtribe Xerantheminae Cass. as subtribes of the tribe Cynareae. Many members of Cassini's tribe Carlineae were treated under the subtribe Carduinae, while two new subtribes, Cardopateae Less. and the Othonninae Less., were proposed for other representatives of this group.

With few exceptions, A. P. de Candolle, among others, accepted Lessing's broad view of the Cardueae. De Candolle reduced subtribe Othonninae to a division of the Calenduleae, elevated three of Lessing's divisions (Carlineae, Serratuleae, Silybeae) to subtribal status and extracted a twelfth subtribe (Carthaminae) from Lessing's subtribe Centaurieae.

As treated by Bentham (1873a), the Cardueae ("Cynaroideae") contained nearly 36 genera in the four subtribes Carduineae, Carlineae, Centaurieae, and Echinopsideae. Lessing's subtribes Cardopatiinae and Xerantheminae (sensu De Candolle) were incorporated into the subtribe Carlineae, while De Candolle's subtribes Carthaminae and Silybinae were included in the Centaurieae and Carduineae, respectively. Similarly, the subtribe Serratulinae (Less.) DC. was divided between the Carduineae and Centaurieae. Cassini's tribes Arctotideae and Calenduleae were resurrected from the subtribal status accorded them by Lessing and De Candolle.

Cassini's system was considered to be a "natural" one by Dittrich (1977), who divided the Cardueae into tribes Echinopeae [sic] (2 genera), Carlineae (11 genera), and Cardueae (66 genera). These he grouped together under the subfamily name Cynaroideae, a name used by Bentham at the tribal level, but without any prior usage at the subfamilial level known to the present author. Dittrich noted that no single character unites the three tribes as he delimited them, not even the traditional stylar character, which he found to be limited to the Cardueae *sensu stricto,* and that between these three groups no connecting forms are known. The Echinopseae are distinguished by their globose, secondary heads comprised of numerous uniflorous heads and by their corollas

with long, slender lobes. The Carlineae have capitula with numerous florets, characteristically short corolla lobes, and receptacles with connate paleae. The Cardueae have long, slender corolla lobes, bristly receptacles, flat and elliptical style branches (in contrast to the half-cylindric or cylindric, usually acuminate branches of the other two tribes), papillose to hairy anther filaments, and laterally compressed achenes. Dittrich further divided the Cardueae into the Carduinae and Centaureinae on the basis of characteristics of the pappus (bristles of almost equal length and form vs. bristles or scales elongated from outside to inside; the internal pappus elements often morphologically different from the outer, forming a "double pappus") and the detachment areas of the achenes (straight, lateral-adaxially, rarely basally oriented vs. always concave and of lateral-adaxial orientation). Whereas Bentham recognized 10 genera of the subtribe Centaureinae, Dittrich (1977) recognized 27, many of which are segregates from *Centaurea*.

In a chemical review of the Cardueae *sensu lato,* H. Wagner (1977) preferred to view the group as comprising two tribes, the Carlineae and the Cardueae. The Echinopseae are apparently treated as a subtribe of the Carlineae, while the Cardueae are divided into two subtribes, the Carduinae and the Centaureinae. The taxa of both tribes are inclusively referred to as the Cynareae throughout his paper.

As delimited by Bentham (1873a), the Cardueae comprise the largest tribe of Compositae in the North Temperate region of the Old World. Bentham thought that the tribes with the closest connections to the Cardueae (Cynareae) were the principally South American Mutisieae (subtribe Gochnatinae) and the South African Arctotideae (subtribe Gorterinae). The latter tribe he considered to be a possible link between the northern tribes Cardueae and Anthemideae.

On the basis of seed anatomy, Lavialle linked the Cardueae (Cynarées) to the Mutisieae (Mutisées) through *Xeranthemum* L. Cronquist (1955, 1977) reaffirmed the close relationship between Mutisieae, Vernonieae, Arctotideae, and Cardueae, but disagreed with Carlquist (1961, 1976), who grouped them with the Lactuceae in subfamily Cichorioideae. While the close relationship of the Arctotideae and Cardueae is not disputed, the position of the Arctotideae was considered problematic by Cronquist (1955, 1977), since he considered them a bridge between the radiate and discoid tribes.

Carlquist (1976) proposed two subfamilies for the Compositae (Asteraceae) and aligned the Cardueae with tribes Arctoteae, Lactuceae ("Cichorieae"), Eupatorieae, Vernonieae and Mutisieae in the subfamily Cichorioideae ("the mutisioid line" vs. the subfamily Asteroideae or "helianthoid line"). Both Carlquist (1976) and Jeffrey (1977) have suggested that the ligulate flowers of the Cichorioideae are modified bilabiate flowers distinctly different and of a separate origin from the ray flowers found in the Asteroideae. Carlquist considered the expanded flowers found in the Arctoteae and Cichorioideae to have originated in the same manner and included the Arctoteae in this subfamily. Cronquist (1977) disputed Carlquist's conclusions about the Arctotideae on the grounds that the external morphology of the ray flowers found in many representatives of the Arctoteae is much like that of the Asteroideae and that Carlquist rested his opinions concerning the alignment of the Arctoteae on

Didelta tomentosum Less., the ray flowers of which have three, four, or five teeth. Carlquist (1976) thought that the Cardueae originated in the Old World (Northern Hemisphere) and that the Arctoteae are the result of "explosive evolution of a stock related to a cichoriead-carduaead complex in southern Africa." While warning that wood anatomy is not a particularly good character on which to establish tribal relationships, Carlquist (1965) noted that the wood anatomy of the Cardueae would not contradict Bentham's (1873b) proposed relationships between the tribes Cardueae, Mutisieae, and Vernonieae.

Jeffrey (1978) recognized 17 tribes and the two subfamiles Lactucoideae (correctly, Cichorioideae Kitamura) and Asteroideae in his treatment of the Asteraceae. He placed the tribes Cardueae and Arctoteae in subfamily Lactucoideae, along with tribes Lactuceae, Arctoteae, Eremothamneae (a monotypic tribe from South Africa), Vernonieae, Liabeae, and Eupatorieae. The Cardueae were said by Jeffrey to have three subtribes that we may presume to be Carduinae, Centaureinae, and Echinopsinae, since he did not follow Dittrich's recognition of the Echinopseae at the tribal level.

In a study of particular interest, Bremmer tacitly supported Dittrich's division of the Cardueae into three tribes. Bremmer contended that the phylogenetic relationships between the Arctoteae and Dittrich's three tribes are unclear and that the Echinopseae, Carlineae, and Cardueae are conceivably monophyletic taxa. If Dittrich's three tribes are treated as a single tribe from which the Arctoteae are excluded, Bremmer claimed that the Cardueae *sensu lato* may not represent a monophyletic group. This is illustrated in the cladogram presented by Bremmer in which the four groups are shown as independent lineages arising from a common ancestor. The Cardueae *sensu stricto* were characterized by three unique characters: 1) papillose to hairy anther filaments, 2) testa epidermal cells in a lignified palisade layer, becoming hard and dark brown to black, and 3) nuclear endosperm. The Echinopseae were distinguished by their secondary heads composed of numerous uniflorous heads and by echinopsine alkaloids, but they were noted as lacking the lactiferous tissue typical of other members of the subfamily Cichorioideae. Neither the Carlineae nor the Arctotideae are delimited by unique characters. The Carlineae are set off as having paleaceous receptacles and shortly lobed disc corollas, while the Arctotideae are said to have true apically three-lobed ray florets and to lack the caudate anthers found in the other three tribes.

Haslett *et al.* and Boulter *et al.* used the analysis of plastocyanin amino acids extracted from species representing eight tribes of the Compositae in a phylogenetic study of the family. Their data support the view that the Compositae are a natural group and indicate a close relationship between the Lactuceae and Cardueae. Indicative of the Cardueae's possibly primitive position among the Compositae was the basal position occupied by *Centaurea* in the phylogeny generated from the data of Boulter *et al.* Bremmer noted that the Cardueae and Lactuceae are the only "cichorioid" tribes included in these studies and that the positions of *Senecio* L. and *Taraxacum* Wigg. indicate a lack of sufficient data from which to draw an unequivocal conclusion.

Support for the primitive position of the Cardueae can be inferred from Bolick's studies on the pollen of Compositae. Bolick described two basic pollen

types in the Compositae: a caveate Helianthoid pattern and a non-caveate Anthemidoid pattern, which Bolick claimed to be less specialized in its structure than the Helianthoid type. The Cardueae were found to have Anthemidoid-type pollen similar to that of the Mutisieae and Vernonieae. Helianthoid pollen is characteristic of the remaining tribes, except for the Anthemideae, Arctoteae, and Lactueae, tribes in which both types of pollen were found.

Recent analyses of chloroplast DNA (Jansen & Palmer) support the hypothesis that the Mutisieae (subtribe Barnadesiinae), not the Cardueae, may be the most primitive subtribe of the family, since members of this tribe lack in their chloroplast genome an inversion characteristic of the other members of the family. The phylogenetic interpretations of Jansen & Palmer have been questioned by Robinson, who showed, in figure form, a hypothetical phylogeny based on Jansen & Palmer's proposal that closely aligned the Cardueae with the Mutisieae (save for the subtribe Barnadesiinae).

Wagner characterized the chemistry of the group as being for the most part similar to the rest of the family. He reported volatile and non-volatile terpenoids, acetylenes, phenolic compounds, and especially hydroxycinnamic acid derivatives and flavonoids as characteristic compounds of the tribe. In addition to a variety of common monoterpenes and triterpenoids of the beta-oleanane and lupane type, Wagner noted that sesquiterpene lactones of the germacrane type are characteristic of the Carduinae and Centaureinae. Further discussion of the structural similarities of these compounds can be found in Hermout & Šorm, who noted that the germacranolides isolated from the Cardueae are strikingly uniform in their structure. The guaianolides cynaropicrin and costuslactone have been found in *Cynara* L. and *Saussurea* DC., while elemanolides have been found in *Centaurea* species. Seaman suggested that the presence of certain C-6 *trans*-lactonized guaianolides and germacrolides and occasionally elemanolides found in 11 genera of the Cardueae may be useful in determining tribal limits. Wagner (1977) noted that the subtribe Centaureinae seemed to be the best differentiated in that in this group are found nearly all types of acetylenes found in the Cynaroideae, a variety of highly methoxylated flavonoids (including flavanones and lignans) and sesquiterpenoids. Whereas the Carduinae contain special acetylenes (e.g., C_{17} acetylenes, acetylene glycosides), sesquiterpenoids of the guaianolide type, monomethoxylated flavonoids, and simple cinnamic acids and derivatives, the Centaureinae have acetylene aldehydes, acetylene chlorohydrins and acetates, sesquiterpene lactones of the germacranolide type, highly methoxylated flavonoids, and typical fully methoxylated lignans. Nowak and coworkers have indicated that cynaropicrin may prove to be a chemical marker for subtribe Centaureinae.

Acetylenes appear to be well differentiated among the subtribes of the Cardueae (Bohlmann *et al.*). Thiophenes in considerable variety were said to be typical of *Echinops* and *Xeranthemum,* furan derivatives were found among members of the Carlininae (*Carlina* L., *Atractylis* L.), and ene-tetrayenes are common constituents in members of the Carduinae (*Arctium, Carduus, Cirsium, Silybum, Onopordum*). While the Centaureinae are not well differentiated chemically from the other subtribes, they do have unique chlorohydrines and -acetates (*Centaurea, Carthamus* L.) not found in the other subtribes, as well as unsaturated aldehydes in the aerial parts and ene-tetrayene-ene in the roots.

Flavonoids occur predominantly as flavones and flavonols (flavanones and flavanonols are restricted to *Carthamus, Centaurea* and *Silybum*). *Silybum* is unique in the tribe in that it produces flavonolignans. Highly methoxylated flavonols and flavones are commonly found in *Centaurea* and *Cirsium.* Wagner further reported that flavonoids are normally found in the glycosidic form with 3-O-glycosides and 4′-O-glycosides as the most common forms.

Other phenolic compounds reported by Wagner for the Centaureinae and Carduinae are cinnamic acids and their derivatives. Tannins are generally absent or occur sporadically. Species of *Arctium, Carthamus,* and *Centaurea* have the dimeric phenylpropane derivatives arctiin and hydroxyarctiin. These compounds were reported to be of physiological importance in the seeds of these taxa and were thought to be restricted to the Carduinae and Centaureinae (Wagner).

Alkaloids are widespread in the Cardueae, but the structures of only a few have been elucidated (Wagner). Amines and cyanogens appear to occur sporadically with only tyramine and histamine reported from *Silybum* and choline from *Onopordum, Saussurea,* and *Centaurea* (Wagner).

Moore & Frankton (1962) proposed a base chromosome number of 17 for the tribe. They suggested that lower numbers have been derived through reduction brought about by translocations with a possible loss of non-essential chromatin and inactivation of excess centromeres. They further noted that this process has occurred in many genera and may have contributed to speciation. They thought that genera with the same chromosome number are not necessarily closely related, nor are those with different chromosome numbers distantly related, since different chromosome numbers do not prevent ready hybridization between taxa. They stressed the importance of evaluating both chromosome morphology and chromosome number when assessing generic relationships.

Achene characters have proved to be the most reliable ones in the delimitation of genera within the Cardueae and have been the subject of several in-depth studies (Dittrich, 1968a & b, 1970; Isley; Lavialle; Singh & Pandey). The four subtribes of the Cardueae are readily distinguished on the basis of their achenes. According to Lavialle and Dittrich, achene characters clearly segregate the Echinopsinae and Carlininae from the closely aligned Carduinae and Centaureinae. Pappus characters and those of the apical region of the achene allowed Dittrich (1970) to distinguish three groups of genera within the Carduinae: 1) *Cirsium, Carduus,* and *Silybum,* 2) *Cynara, Notobasis* Cass., *Ptilostemon* Cass., *Arctium,* and *Onopordum,* 3) *Galactites* Moench, *Picnomon* Adanson, *Tyrimnus* Cass., and *Jurinea* Cass. Dittrich's study (1968a & b) of the Centaureinae informally grouped taxa of this subtribe on the basis of whether the hilum was basal (e.g., *Serratula* L., *Rhaponticum* Hill, *Leuzea* DC.), lateral (*Carduncellus* Adanson, *Carthamus,* sections of *Centaurea*), or caudate (*Cnicus,* sections of *Centaurea*).

The Cardueae have economic significance in several areas, perhaps, most notably, as a source of noxious weeds that have overgrown much agricultural land throughout the world. Species of *Centaurea, Cirsium, Echinops,* and other genera of the tribe are cultivated as ornamentals. *Cynara Cardunculus* L., the cardoon, has long been cultivated for the petioles of its leaves that are eaten

like celery. The bracts and the receptacle of immature heads of *C. Scolymus* L., which is probably derived from *C. Cardunculus,* are commonly eaten as the globe artichoke. Species of *Centaurea* have been noted as important sources of nectar for honey bees (Goltz).

Echinops, a genus of about 120 species (Mabberley) distributed in southern Europe, North Africa, temperate and subtropical Asia, northward to Japan, and naturalized in parts of North America, has been included by Cronquist (1980) as a member of the flora of the southeastern United States. Three species of the genus (*E. sphaerocephalus* L., *E. exaltatus* Schrader, and *E. bannaticus* Rochel ex Schrader) are often grown as ornamentals (*E. bannaticus* frequently as *E. Ritro* L.; see Karlsson). Cronquist (1980) noted that *E. sphaerocephalus* has escaped from cultivation and become casually established in parts of the United States and southern Canada. *Echinops sphaerocephalus* is the only species of *Echinops* treated in floras of the northeastern United States (e.g., Fernald; Gleason & Cronquist), but it has not been included in any of the floras for the Southeast (e.g., Chapman; Long & Lakela; Radford *et al.*; Rickett; Small, 1933, among others), nor have I seen specimens that would indicate that *E. sphaerocephalus* has become established in the Southeast. Since the three species mentioned above are commonly cultivated, it is reasonable to expect that one or more of them may eventually become established in some areas of the Southeast. *Echinops* is included here in brackets in the key to genera, and various selected references are among those that follow.

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Key to the Genera of Cardueae in the Southeastern United States

A. Achenes attached to the receptacle by the base; flowers all alike, marginal ones not enlarged.
  B. Heads 1-flowered, united into a spherical, secondary head. ..... [*Echinops.*]
  B. Heads with more or less numerous flowers, not united into a secondary head.
    C. Receptacle fleshy, deeply alveolate, naked or only very shortly bristly; plants with strongly spiny-winged stem and tomentose herbage. . 4. *Onopordum.*
    C. Receptacle with scales or setae or densely bristly; plants without both stem strongly spiny winged and herbage tomentose throughout.
      D. Staminal filaments united below; leaves white mottled. ...3. *Silybum.*
      D. Staminal filaments separate; leaves not white veined or variegated.
        E. Involucral bracts hooked at tip; leaves not bristly or spiny, the lower broadly ovate and mostly cordate; style branches partly distinct. ... . 5. *Arctium.*
        E. Involucral bracts not hooked; leaves bristly or spiny on the margin, lanceolate or narrow; style branches coherent, commonly with a pubescent ring at base.
          F. Pappus bristles plumose; stem not conspicuously spiny winged (except in *C. vulgare*). ..... 1. *Cirsium.*
          F. Pappus bristles barbellate, not plumose; stem conspicuously spiny winged. ..... 2. *Carduus.*

A. Achenes obliquely or laterally attached to the receptacle; marginal flowers often enlarged and neutral, appearing ray-like, occasionally undifferentiated from inner florets.
  G. Achenes with 10 horny teeth at the summit, and with a biseriate pappus of 10 long awns alternating with 10 shorter inner ones; leaves prickly margined; flowers yellow. ..... 7. *Cnicus.*
  G. Achenes without horny apical teeth, and with a pappus of several series of short (seldom elongate) scales or bristles, or the pappus wanting; leaves not prickly; flowers in most species anthocyanic (or white), seldom yellow... 6. *Centaurea.*

Subtribe CARDUINAE Dumortier, Fl. Belg. Prodr. 72. 1827.

1. **Cirsium** Miller, Gard. Dict. Abridg. ed. 4. **1:** ord. alph. 1754, emend. Scopoli, Fl. Carniol. ed. 2. 123. 1772.

Biennial or perennial [annual] herbs. Stems to 2.5 m tall, branched or simple, arachnoid-tomentose to glabrous, unarmed or spiny winged, wings triangular with a short apical spine. Leaves sessile to long petiolate; blades lanceolate to oblanceolate, the upper surface glabrescent or setaceous [densely pubescent], glandular, or glandular-pubescent, lower surface glabrescent or pubescent along the primary veins to white-tomentose throughout, glands capitate or punctate, hairs crispate or sinuate, multicellular; margins entire to more often incised or laciniate, weakly to strongly spiny. Capitula (heads) homogamous or heterogamous, discoid, ovoid to globose, terminal or axillary, solitary or in clusters of 3 to several heads on short to somewhat elongate peduncles [sessile]. Involucre ovoid, to ca. 7 cm high and ca. 9 cm wide, bracts imbricate, multiseriate, linear-lanceolate to lanceolate, acute to acuminate, often spine tipped, usually with a simple apical spine, adpressed to reflexed, glabrous to sparsely pubescent [arachnoid-pubescent], often with a glutinous dorsal ridge (vitta), entire or ciliate [lacerate]. Receptacle flat to subconic, scales numerous, setaceous. Flowers perfect (rarely imperfect and then the heads functionally so and the plants partly or wholly dioecious). Corollas tubular, actinomorphic, white, cream-yellow, lavender, purple, or garnet red [red], glabrous or sparsely glandular, tube narrow, elongate, throat short, undivided, lobes linear to lanceolate, elongate. Staminal filaments glabrous to more often papillose-hairy, anthers white or stramineous, saggitate, apical appendage acute, small. Styles smooth below a distinct collar of hairs, branches papillate, scarcely divergent, narrowly truncate to acute. Achenes 3–6 mm, basifixed or nearly so, glabrous, smooth, oblong, compressed, gibbous, with a distinct, apical margin surrounding a subconical central projection. Pappus of several rows of distinctly plumose setae, basally fused, deciduous as a ring [or persistent]; the inner setae somewhat longer than the outer and simple, lanceolate, occasionally flattened and ciliate towards apex; pappus of outermost florets often with fewer, minutely barbellate or scabrous setae. LECTOTYPE SPECIES: *Cirsium heterophyllum* (L.) Hill. (*Carduus heterophyllus* L.) = *Cirsium helenioides* (L.) Hill; see Britton & Brown, Illus. Fl. No. United States, Canada. ed. 2. **3:** 548. 1913; Britton & Millspaugh, Bahama Flora, 458. 1920; R. McVaugh, Flora Novo-Galiciana, 229. 1982. Werner treated *Cirsium heterophyllum* as a synonym of *C. helenioides* (L.) Hill in *Flora Europea.* (Name Latin, from *cirsion,* thistle, used by Dioscorides, from *kirsos* or *cirsos,* a swollen vein, which it was said to cure; see Loudon; Fernald; Correll & Correll; Munz.)—THISTLE, PLUMED THISTLE.

Tenuous morphological distinctions and a misunderstood nomenclatural history have led authors to treat members of *Cirsium* as representatives of both *Carduus* (Elliott; Nuttall; Radford *et al.*) and *Cnicus* (Gray, 1874; Pammel, 1901). Linnaeus did not recognize *Cirsium,* but described the species later treated as *Cirsium* as representatives of *Carduus.* The year following the publication of *Species Plantarum,* Miller proposed *Cirsium* on the basis of char-

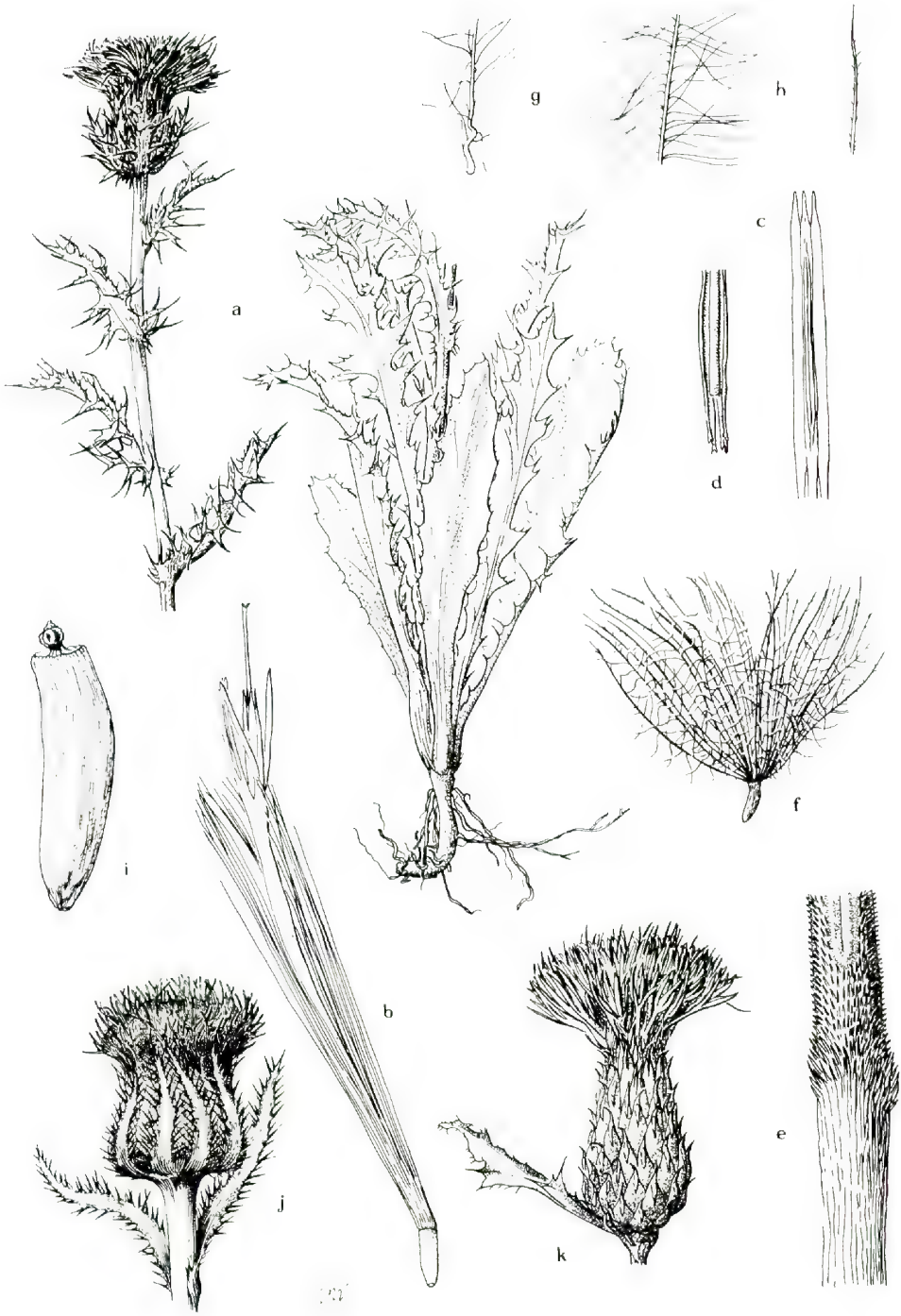
acteristics of the spines on the leaves and the lack of spines on the "cup of the flower" (i.e., involucre). Miller used polynomials under his generic descriptions until the 1768 edition of *The Gardener's Dictionary* (see Druce for commentary), yet in this edition Miller merged *Cirsium* with *Carduus*. Because of this, it was Scopoli (1772) who provided the first binomials in *Cirsium* and who noted the plumose pappus as a distinguishing character for the genus. Adanson was wrongly credited as the author of *Cirsium* for his realignment of *Cnicus* Tournefort (*Cnicus* L. is now a conserved name). Primarily on the basis of characters of the achene, Cassini, Lessing, and De Candolle considered *Cirsium* to be closely related to *Carduus*, but distant from *Cnicus*. Bentham and Asa Gray (1874) both included *Cirsium* in *Cnicus*, but Hoffmann maintained its generic status. Dittrich (1977) assigned *Cirsium* and *Carduus* to the tribe Cardueae (subtribe Carduinae Dumort.) and aligned them with *Modestia* Charadze & Tamamshian (a genus of three species of Central Asia) and *Silybum* on the basis of achene characters (apical plate, pappus, and detachment area).

While the division between *Cirsium* and *Carduus* has long been noted as somewhat arbitrary (cf. Scopoli, 1772; McVaugh) and various authors (e.g., Correll & Johnston; Willis) have suggested that *Cirsium* should be included within *Carduus*. Ahles in Radford *et al.* (1968) is the only recent author who has adopted this position. Recent floras of Europe (e.g., *Flora Europaea, Flora of Turkey, Flora Iranica*) and the Orient have maintained *Cirsium* and *Carduus* as separate genera.

A number of sectional names have been proposed for *Cirsium* since Dumortier first subdivided the genus into sections *Eriolepis* (Cass.) Dumort. (involucres woolly), *Onotrophe* (Cass.) Dumort. (involucres spiny), and *Cirsiotypus* Dumort. (involucres unarmed). Dumortier was followed shortly by Duby, who borrowed on De Candolle's unpublished material and described the sect. *Epitrachys* DC. ex Duby (leaves with upper surface spiny; flowers purple).

In a treatment that has gone largely unrecognized, George Don (in Loudon) divided *Cirsium* into seven sections: *Solitaria* (leaves decurrent; flowers red, heads subsolitary), *Polyanthema* (leaves decurrent; flowers red, heads aggregated), *Leucanthum* (leaves decurrent; flowers whitish), *Eriophora* (leaves sessile; flowers red, heads subsolitary), *Aggregata* (leaves sessile; flowers red, aggregated), *Chrysantha* (leaves sessile; flowers yellow or white), and *Dubia*. Don's sect. *Eriophora* contained several species found in the southeastern United States (*C. discolor, C. altissimum, C. muticum* Michaux, *C. virginianum* (L.) Michaux, *C. arvense* (L.) Scop.), as well as the species later chosen as lectotype of the genus. Don's treatment of other families had closely followed De Candolle's accounts published in his *Prodromus*, but his treatment of the Compositae preceded De Candolle's by several years.

De Candolle recognized six sections: *Lophiolepis* (Cass.) DC., *Eriolepis, Orthocentron* (Cass.) DC., *Corynotrichum* DC., *Cephalonoplos* DC., and *Onotrophe* DC. The last section contained several species (*C. repandum* Michaux, *C. horridulum* Michaux, *C. muticum, C. virginianum*) from the southeastern United States, and, along with Don's sect. *Eriophora*, is currently placed in synonymy under sect. Cirsium. Koch, who claimed to have based his treatment on a manuscript of De Candolle's treatment of Compositae for the *Prodromus*,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attributed two sections to De Candolle (*Epitrachys, Chamaeleon*) that De Candolle did not recognize, and erected yet two others (*Breea* (Less.) Koch and *Picnomon* (Cass.) Koch), each of which contained a single species (*C. arvense* and *C. acarna* DC., respectively). Koch's sect. *Chamaeleon* was later placed in synonymy under sect. CIRSIUM, and his sect. *Breea* is considered to be a synonym of sect. CEPHALONOPLOS, a section set aside for dioecious species.

Although Bentham (1873a) did not produce a sectional treatment of *Cirsium,* Hoffmann, whose treatment of the Compositae bore many similarities to Bentham's, recognized seven sections of *Cirsium*: *Notobasis* (Cass.) Hoffm., *Cephalonoplos* DC., *Epitrachys* DC. ex Duby, *Chamaeleon* DC. ex Koch, *Erythrolaena* Don in Sweet, *Ptilostemon* (Cass.) Hoffm., *Lamyra* (Cass.) Hoffm., and *Ancathia* (DC.) Hoffm.

Petrak (1917), the most recent monographer of *Cirsium,* considered the American species to be members of subgenus *Eucirsium* (= CIRSIUM) in which he recognized six sections for the North American taxa: *Cirsiopsis* Petrak, *Mastigophyllum* Petrak, *Dermatolepis* Petrak, *Echenais* (Cass.) Petrak, *Onotrophe* and *Erythrolaena* (see Ownbey & Hsi). The nearly 15 indigenous species known from the Southeast (excluding two European introductions) were placed in three subsections of sect. *Onotrophe* (Petrak, 1917; Frankton & Moore, 1969; Ownbey & Olson), a section later considered to be a synonym of sect. CIRSIUM (Petrak, 1979).

The two naturalized European species (*Cirisum arvense* (L.) Scop. and *C. vulgare* (Savi) Tenore) are not considered to be closely related to the native species of the Southeast. Werner included *C. vulgare* in sect. *Eriolepis,* but Petrak (1979) placed this species in sect. *Epitrachys* subsect. *Lanceolata* Petrak. While the name *Epitrachys* may more closely characterize the group of taxa included under this name, Petrak's description of *Epitrachys* and Werner's description of sect. *Eriolepis* are not easily distinguished. As treated by Werner, the sect. CIRSIUM includes *C. helenioides* (L.) Hill under which he synonymized *C. heterophyllum,* the taxon previously designated as the lectotype species for the genus (see above). *Cirsium arvense* was retained in sect. CEPHALONOPLOS DC. by both Petrak (1979) and Werner.

Of the nearly 75 species of *Cirsium* recognized in the continental United States, only 12 to 15 are native to the Southeast. Many are biennials or mono-

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FIGURE 1. **Cirsium.** a–i, *C. vittatum*: a, small flowering plant, base of plant to right, upper part with flowering head to left, × ½; b, flower, showing protruding stamens and style, × 2; c, three of the five anthers from within, the central one in more detail, × 4; d, base of an anther from within to show appendages, filament removed, × 10; e, detail of style, showing stylar brush at middle and lowermost part of united style arms with stigmatic line, × 30; f, achene with pappus, × 1; g, h, basal, central, and distal portions of a single pappus filament, × 4; i, achene from which pappus has become detached, × 5. j, *C. horridulum*: flowering head, showing conspicuous false involucre, × ½. k, *C. Lecontei*: flowering head, the cobwebby hairs omitted, × 1.

carpic taxa that need three to five years to come to flowering and fruition. Petrak (1917) treated the southeastern taxa in three subsections (*Odorata, Campanulata,* and *Acanthophylla*) of sect. ONOTROPHE DC. Taxa of subsections *Odorata* and *Campanulata* tend to inhabit the Atlantic and Gulf Coastal Plains and are often associated with salt or fresh marshes, bogs, savannas and pine barrens. The subsection *Acanthophylla* includes taxa often found in woodlands, thickets, and pasture areas of the Piedmont of Georgia and the mountains of Kentucky, Tennessee, and Arkansas. Cytological studies (Ownbey & Hsi; Ownbey & Olson; Moore & Frankton, 1969) have indicated that species of subsect. *Odorata* have chromosome numbers of $2n = 30$ and above, while those of subsections *Campanulata* and *Acanthophylla* have lower chromosome numbers ($2n = 18, 20$).

Recent treatments of the species of *Cirsium* in the eastern and southeastern United States have followed Petrak's taxonomic system, except for a realignment of two species at the subsectional level (Ownbey & Olson). The transfer of *C. Lecontei* Torrey & Gray and *C. repandum* Michaux from subsect. *Campanulata* to subsect. *Odorata* was made on the basis of their apparent cytological homogeneity with the other species (*C. horridulum* Michaux, *C. pumilum* (Nutt.) Sprengel, *C. vittatum* Small) of the latter subsection. The transfer of *C. repandum* and *C. Lecontei* left *C. Nuttallii* DC. the lone member of subsect. *Campanulata,* a group initially characterized by oblong-cylindrical or campanulate capitula.

Cirsium repandum, C. Nuttallii, and *C. Lecontei* are morphologically similar species often found growing in sandy soils of pine barrens and savannas of the Coastal Plain. *Cirsium Lecontei* appears to inhabit somewhat wetter habitats (edges of swamps, peat bogs, low, moist meadows) than the other two species, which occur in open pine woodlands, on sand ridges, and along roadsides. All three species flower primarily from mid-June to mid-September (Cronquist, 1980; Radford *et al.,* 1968). No occurrence of hybridization among these species has been reported. Moore & Frankton (1969) considered *Cirsium repandum* and *C. Lecontei* to be uniform species that show characteristics of other species groups, but remain strikingly distinct. They suggested that *C. repandum* may have developed from hybridization between the similar more northern species *C. pumilum* and the *C. horridulum* complex (Moore & Frankton, 1969), a group that Petrak (1917) and Moore & Frankton believed to be unrelated in origin to other North American species.

Several taxa (e.g., *C. horridulum, C. Smallii* Britton, *C. vittatum*), recognized as series *Horridula* of subsect. *Odorata,* form a distinct group easily recognized in the field by the presence of a large false involucre (Moore & Frankton, 1969). Elements of this complex, distinguished from one another by one or two subtle characters (Cronquist, 1980), can be found along the Atlantic and Gulf Coastal Plains from Maine to Mexico in the sandy soil of low pine woods, savannas, or along the edges of fresh or salt marshes.

Chromosome numbers of $2n = 30$ were reported for *C. pumilum* and *C. repandum,* $2n = 32$ for both *C. Lecontei* and *C. horridulum,* and $2n = 32, 34$ (33, 35) for *C. vittatum* (Ownbey & Olson). Moore & Frankton (1969) reported $2n = 28$ for *C. Lecontei* and suggested that this species arose from a past

hybridization between stock of the series *Horridula* and *C. Nuttallii* (subsect. *Campanulata*). Two chromosome numbers ($2n = 24$ and $2n = 28$) were reported for *C. Nuttallii,* and probable accessory chromosomes were observed in association with 12 bivalents in a plant from Florida, yet normal meiosis was noted among 14 bivalents in plants from Louisiana. Ownbey & Olson investigated plants of *C. Nuttallii* from populations in Florida, Georgia, and South Carolina and found the chromosome number to be consistently $2n = 24$, except for one plant from Georgia with a chromosome number of $2n = 26$.

Included in a third subsect., *Acanthophylla,* were four species from the Southeast (*C. altissimum* (L.) Sprengel, *C. discolor* (Muhl.) Sprengel, *C. muticum* Michaux, *C. virginianum* (L.) Michaux). This subsection was differentiated primarily by ovate to ovate-globose capitula and weakly spiny involucres (Petrak, 1917). Later, *C. carolinianum* (Walter) Fern. & Schub. and *C. terraenigrae* Shinners (= *C. Engelmannii* Rydb.; see Shinners, 1964) were added to this subsection (Ownbey & Olson). Many of the taxa comprising the subsection inhabit inland woods, thickets, and pasture areas of higher elevations and, in some cases, have become ready colonizers of disturbed areas. *Cirsium muticum* is found in swamps and moist woods from central Canada to New Brunswick, south to the Gulf Coast, and west to eastern Texas. *Cirsium discolor* occurs in drier habitats, mostly thickets and grasslands, from New England south along the Atlantic Coast to North Carolina, west to Tennessee, and north to Minnesota. The closely related *C. altissimum* (L.) Spreng. occupies slightly more shaded, but otherwise similar habitats to those of *C. discolor* (see, Ownbey, 1964). The distributional range of *C. altissimum,* from southern New York to northern Florida, west to the Dakotas and Texas, is more southerly than that of *C. discolor.* According to Frankton & Moore (1963), this southern extension of *C. altissimum* may be attributed to the reduction of the diploid chromosome number from 20 to 18 and the coincident plasticity that produced the southern phenotypes of *C. altissimum,* which are sometimes recognized as species.

Subsection *Acanthophylla* appears to be morphologically and cytologically homogeneous. At least three species (*Cirsium carolinianum, C. muticum, C. discolor*) have chromosome numbers of $2n = 20$. Extra chromosomes arising from meiotic irregularities and triploid populations have been reported for *C. muticum* (Frankton & Moore, 1963; Ownbey & Olson), which is known to hybridize with *C. discolor* (Ownbey, 1951; Bloom). In turn, *C. discolor* has been shown to hybridize with *C. altissimum,* $2n = 18$ (Ownbey, 1964), the two not easily distinguished in parts of their ranges (Davidson) and considered to be conspecific by some authors (e.g., Gray, 1884b; Wiegand & Eames). More than 98 percent of both pollen and achenes produced by the progeny of the cross between *C. discolor* and *C. altissimum* aborted before maturation, yet rare instances of introgression were reported (Ownbey, 1964). A similar pattern was found in the hybrid progeny of the *C. muticum* × *C. discolor* crosses. In this case, the hybrids produced less than three percent fully formed pollen (vs. over 90 percent for the parental species), and less than five percent of the flowers in hybrids produced mature achenes; yet some evidence of introgression of *C. discolor* into *C. muticum* was reported (Ownbey, 1951).

On the basis of concepts set forth in an earlier paper (Moore & Frankton, 1962b), Frankton & Moore (1963) considered *Cirsium discolor* and *C. altissimum* to be slightly more advanced morphologically than *C. muticum,* because of the number of pappus setae and the length of the corolla tube relative to the rest of the corolla. Petrak placed *C. discolor* and *C. altissimum* in the series *Altissima* and *C. muticum* alone in the series *Mutica,* an arrangement with which Frankton & Moore (1963) concurred. More recently, these three species, along with *C. Engelmannii* Rydb. (*C. terrae-nigrae* Shinners) and *C. carolinianum,* were grouped in the series *Altissima* (Ownbey & Olson).

Cirsium virginianum (L.) Michaux, a species of the Atlantic Coastal Plain that inhabits savannas, bogs, and wetlands from New Jersey to northern Florida, is morphologically similar to *C. carolinianum,* a species that occurs in open woods on dry, sandy soils from southern Ohio to the mountains of North Carolina, northwestern Georgia, Alabama, Arkansas, Louisiana, and eastern Texas. *Cirsium virginianum* has been reported to have chromosome numbers of $2n = 28$ (Ownbey & Olson; Moore & Frankton, 1969) and $n = 11$ (Jones, 1968), while *C. carolinianum* has been reported as $2n = 20$ (Ownbey & Olson) and $n = 11$ (Jones, 1970). Ownbey & Olson included *C. carolinianum* in series *Altissima,* but left *C. virginianum* in series *Virginiana* where it was initially placed by Petrak. *Cirsium virginianum* was not considered by them to be closely allied to other species of the Southeast, and its relationships to other North American species were considered to be obscure (Ownbey & Olson).

Cirsium arvense (L.) Scop. is a widespread, pernicious weed that occurs in fields and wasteplaces across the northern half of Europe and the United States. It extends south into Iowa (Pammel; Hayden) and Kansas (Barkley) and west to California, but it only skirts the northern part of the Southeast: northwestern North Carolina, northern Tennessee, and northwesternmost Arkansas (E. B. Smith). This species causes considerable losses in agricultural yields (Hayden; Hodgson, 1958, 1968; U. S. Dep. Agr.), and its control has been the subject of studies too numerous to be accounted for in this treatment (for partial reviews, see Haggar *et al.*; Hodgson, 1968).

The separation of "sexes" in *Cirsium arvense* was first noted by T. Smith (1822), who described in detail the morphological differences between what he considered to be separate "male" and "female" plants. Correns (1916) more accurately described the imperfectly dioecious nature of this species and noted staminate plants bearing seeds of sexual origin. Correns's findings were confirmed by Delannay (1977), who showed that the stigmas of staminate plants are narrower and more elongated and the stigmatic papillae less well developed than on carpellate plants. According to Delannay, the result of these differences is less retention and germination of pollen on the staminate plants. Both Delannay (1977, 1979) and Lloyd & Myall upheld Correns's proposal that dioecy in *Cirsium* evolved from gynodioecy, a condition common to many European species of *Cirsium* (e.g., *C. palustre*; Delannay, 1979). While early studies (Bakker; Correns; Groh; Lloyd & Myall) reported very few occurrences of "hermaphrodites" or strict dioecy among populations of *C. arvense,* Kay took into account that populations of this species differentiate into clones with pollen-bearing flowers and clones with strictly carpellate ones and found that

15 percent of the pollen-bearing clones among three populations in southern Britain were perfect-flowered plants that produced from ten to 65 seeds per capitulum. Another 11 percent were "subhermaphrodites" that produced two to ten seeds per capitulum. Both "hermaphrodites" and "subhermaphrodites" had high seed viability, but experiments in self-pollination resulted in low seed set among the perfect-flowered plants.

Williams studied the germination of achenes of five *Cirsium* species and reported that of those studied *C. arvense* was the most variable, with the percent of germination ranging from 13.4 to 24 in four separate studies. Williams also noted that the achenes of many thistles are commonly parasitized by beetle larvae, fruit flies (*Urophora* sp.), and rusts (*Puccinia* sp.). Guyot & Guillemat recorded a considerable decrease in viability of *C. arvense* seeds over a period of five years (less than ten percent germination after five years). Kumar & Irvine reported an increase in germination rate in *Cirsium arvense* achenes in response to prechilling, photoperiod (eight hours of light), and higher temperatures (30°C). Similar results were reported by Amor & Harris in populations found in Victoria, Australia. Allelopathic properties have been attributed to *C. arvense* by several authors (Amor & Harris; Bendall; Helgeson & Konzak; Stachion & Zimdahl).

Cirsium vulgare, a wind-dispersed, monocarpic, tetraploid ($2n = 68$) weed introduced from Eurasia, is widely established in disturbed areas in much of North America. Although primarily an insect-pollinated outcrossing plant, self-pollination or apomixis has been shown to produce viable, if somewhat fewer, seeds. Achenes produced by either self-pollinated flowers or apomixis were significantly heavier than achenes produced by cross-pollinated flowers. In addition, achenes produced by cross-pollination germinate more slowly, and fewer seedlings survive their first year, than achenes produced by apomixis or self-pollination (Van Leeuwen, 1981b). This led Van Leeuwen to propose that achenes produced by cross-pollination are better dispersed and perhaps better equipped genetically (i.e., genetically more differentiated) to colonize areas apart from the parental plants than are achenes produced otherwise. Predispersal seed predation by birds, mice, and insects (particularly *Cheilosia grossa* and *Epiblema scutulana*) resulted in an average loss of seven percent of the achenes in populations of *C. vulgare.* Stem predation by rabbits and stem-boring insects brought about an average 38 percent loss of flowering heads on these plants (Van Leeuwen, 1981a, 1983). De Jong & Klinkhammer proposed a different hypothesis for the effects of microorganisms on the germination of seeds of *C. vulgare.*

The range of chromosome numbers from $2n = 34$ to $2n = 18$ among species of *Cirsium* has been proposed to be an aneuploid reduction series brought about by translocations between non-homologous chromosomes (Frankton & Moore, 1961; Moore & Frankton, 1962a; Ownbey & Hsi; Bloom). Intraspecific variation in chromosome numbers and accessory chromosomes are considered to be common (Frankton & Moore, 1963; Moore & Frankton, 1962a; Ownbey *et al.*; Pinkava & Keil). American species have been consistently reported to be diploids, while species introduced from Europe (*C. arvense, C. vulgare*) are known to be polyploids (Bloom). Triploid, tetraploid, and hexaploid species (all with multiples of 17 chromosomes) have been noted among Japanese

species (Aishima, Arano). Taxa from the putative center of origin in Eurasia have been reported as diploids ($2n = 34$) or polyploids (Moore & Frankton, 1962a; Ownbey, Raven, & Kyhos; Bloom). Moore & Frankton (1962a) suggested that the European species of *Cirsium* are on the base level of cytological evolution, since they share a base chromosome number of 17.

Few investigations have been made of the phenolic compounds of *Cirsium* species. The flavonoids tricin-5-O-glucoside, quercetin-3-O-digalactoside and quercetin-3-O-rhamnoglucoside were reported as major constituents in *C. arvense* (Wallace). Shelyuto and colleagues (1970, 1972b) isolated apigenin, luteolin, apigenin-7-O-glucoside, apigenin-7-O-rhamnoglucoside and 3-O-methylkaempferol from *C. arvense* (see Wagner for review). The flavonoid cirsimaritin, first found in *C. brevistylum,* was determined to be a minor constituent of *C. arvense,* but was not found in *C. edule, C. undulatum,* or *C. vulgare* (Wallace & Bohm). The flavonoids kaempferol-3-O-glucoside, quercetin-3-O-glucoside, quercetin-3-O-galactoside, apigenin-7-O-diglucoside, and genkwanin-4′-O-glucoside were reported for *C. lanceolatum* (L.) Hill (McGowan & Wallace[3]). The phenolic acids p-coumaric, caffeic, ferulic, p-hydroxybenzoic, protocatechuic and vanillic were also reported for *C. lanceolatum* (McGowan & Wallace). Taraxasterol was found in *C. texanum,* but tests for alkaloids and sesquiterpene lactones were negative for this species (Domínguez *et al.*). Taraxasterol and triterpenes are known from *C. arvense* (Dutta *et al.*), and stigmasterol has been reported from *C. oleraceum* (L.) Scop. (Piatak & Eichmeier). Alkaloids of unknown structure have been found in *C. arvense* and in 12 other species of *Cirsium* (Willaman & Schubert; Willaman & Li).

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2. **Carduus** Linnaeus, Sp. Pl. **2:** 820. 1753; Gen. Pl. ed. 5. 358. 1754.

Biennial [annual or perennial] herbs. Stems to ca. 2 m tall, fibrous, glabrous to arachnoid-tomentose, spiny winged, wings triangular to palmate, occasionally with an apical spine 1–5 mm long. Leaves sessile to more often petiolate; blades lanceolate to oblanceolate, deeply lobed to 2-pinnatisect [subentire], to ca. 25 cm × 10 cm, the upper surface glabrescent to sparsely [densely] pubescent, occasionally punctate glandular, the abaxial surface glabrous to densely arachnoid-villous and often glandular, hairs crispate or sinuate, multicellular, glands capitate or punctate; margins often with an apical spine to 5 mm [exceeding 10 mm]. Capitula homogamous, discoid, subglobose [globose], 1.5–2.5 [8] cm wide, sessile or in clusters of 2–4 [10 or more] on narrowly winged peduncles. Involucre ovoid, bracts imbricate in 5–8 [10] series, linear-lanceolate to oblanceolate, acute to acuminate, spine tipped or sharply mucronate, spreading or reflexed [adpressed], glabrous to densely pubescent, occasionally minutely glandular; margins entire, scabrous or ciliate; outer bracts long-acuminate to acute, inner bracts longer than middle, acute [obtuse], shortly contracted to a spinule, obscurely 1–5 veined, occasionally contracted slightly below middle. Receptacle densely setose. Flowers perfect, actinomorphic or zygomorphic. Corolla purple, lavender, [pink or white], tube narrow, throat short and unequally divided by sinuses of corolla lobes with 2 sinuses deeper than the others, lobes linear, elongate (ca. 4–5 mm long), glabrous or sparsely glandular. Staminal filaments sparsely to densely pubescent, anthers white, sagittate, with slender, entire or lacerate basal appendages, apical appendage acute, small. Styles smooth below a distinct collar of hairs at base of the relatively short, papillose, scarcely divergent, narrowly truncate to acute branches. Achenes basifixed, 3–5 mm long, somewhat compressed, glabrous, smooth [rugulose when dried] with 5–10 ribs and a distinct annular margin at apex. Pappus bristles in several rows, connate at base, unequal, inner setae longer than outer, white, not plumose, smooth to barbellate. LECTOTYPE SPECIES: *Carduus nutans* L.; see Britton & Brown, Illus. Fl. No. U. S. Canad. ed. 2. **3:** 554. 1913. (Name the ancient Latin one.)—PLUMELESS THISTLE.

A genus of 91 species, according to Kazmi (1963, 1964), distributed in Eurasia and northern Africa. Two introduced and naturalized species occur in the southeastern United States.

As established by Linnaeus, *Carduus* was composed of 23 species, several of which were later placed in *Cirsium* by Scopoli (1772) (see discussion under *Cirsium*). While the strength of the characters used to distinguish these genera (pappus of smooth or barbellate setae vs. pappus of plumose setae) has been questioned (Correll & Johnston; Willis) most workers have treated *Cirsium* and *Carduus* separately. Recently, though, Ahles in Radford *et al.* included in *Carduus* 13 taxa that are considered in this paper to be members of *Cirsium.*

The 91 species recognized by Kazmi (1963, 1964) were placed in two subgenera (CARDUUS, AFROCARDUUS Kazmi) of Eurasian and African distribution. He later (1964) proposed a third subgenus (ALFREDIA (Cass.) Kazmi) based on characters of the corolla lobes, staminal filaments, and pappus. Subgenus AFROCARDUUS was delimited by hooked corolla lobe apices, glabrous or sometimes

tuberculate filaments, and opaque achenes. AFROCARDUUS is comprised of ca. 21 African species that are placed among sections ACAULON Kazmi (7 spp.), AFROCARDUUS Kazmi (8 spp.), and PINNATISQUAMA Kazmi (6 spp.). For subg. ALFREDIA, represented by species from Afghanistan, western Pakistan, eastern Russia, Mongolia, Tibet, and China, Kazmi (1964) proposed sections ALFREDIA, PTEROCAULON, and APTERON but did not give a treatment of species. Moore & Frankton (1962) reported that sect. ALFREDIA contains six species distinguished by their yellow flowers.

Subgenus CARDUUS (70 spp.) (Kazmi, 1964) is distinguished by smooth corolla lobes, villous staminal filaments, and pappus usually of whitish or, rarely, stramineous bristles. The distribution of this group extends from the Mediterranean region to northern Europe with several widespread species that are now encountered in many areas of the United States.

The two species *Carduus acanthoides* L. and *C. nutans* L., musk-thistle, known to occur in the Southeast are members of subg. CARDUUS. Both belong to the type section, one of two (CARDUUS, LEPTOCEPHALI Reichenb. f.) recognized in the group (Kazmi, 1964; Franco, 1976). *Carduus crispus* L., a species sparingly introduced in the United States, and also a member of sect. CARDUUS, has not been reported in the Southeast, but eventually may be encountered in the northern parts of the area along roadsides or in disturbed areas (Johnson, 1974).

Both *Carduus nutans* and *C. acanthoides* are widely established in the United States along roadsides and in pastures and disturbed areas. Hensley observed that both species thrive in areas of high-calcium limestone deposited at very shallow depths. *Carduus acanthoides* does not extend south of a few localized occurrences in western North Carolina (Radford *et al.*) and, perhaps, Tennessee, yet *C. nutans* has been collected as far south as Georgia, Mississippi, and Louisiana. Both species are monocarpic, outcrossing (Smyth & Hamrick) biennials that can be differentiated by capitulum and involucre size and the orientation of the capitula (heads nodding in *C. nutans* vs. upright or erect in *C. acanthoides*). Moore & Frankton (1974) recognized three subspecies of *C. nutans* in Canada, and Kazmi (1964) added a fourth from northern Europe. Two subspecies of *C. acanthoides* were described by Kazmi (1964).

Cytological studies have reported chromosome numbers of $2n = 16$ ($n = 8$) for *C. nutans* (Poddubnaja-Arnoldi; Górecka; Löve & Löve, 1944; Moore & Frankton, 1962; Devesa; Van Loon & De Jong; Van Loon & Kieft; Van Loon & Snelders) and $2n = 22$ for *C. acanthoides* (Górecka; Löve & Löve, 1944; Moore & Frankton, 1962; Poddubnaja-Arnoldi; Van Loon & Kieft). Mehra and colleagues and Mehra & Remanandan have reported chromosome numbers of $2n = 40$ ($n = 20$) for *C. nutans* with laggards and bridges mildly disturbing meiosis. The chromosome number for *C. crispus* has consistently been reported as $2n = 18$ (Arano; Górecka; Löve & Löve, 1944; Poddubnaja-Arnoldi; Probatova & Sokolovskaya; Rostovtseva).

Moore & Frankton (1962) suggested a base chromosome number of 8 or 11 for the genus. The lower numbers were thought to result from reduction brought about by fragmentation and fusion. Polyploids appear to be rare in *Carduus*, with $2n = 54$ first reported for *C. tenuiflorus* Curt. and *C. pycnocephalus* L. by

Moore & Frankton (1962). They speculated that these species are hexaploids of the base number 9 formed by hybridization between a diploid and a tetraploid species followed by doubling of the chromosome number of the hybrid.

Hybridization is commonly reported in *Carduus* (Arènes, 1949; Briquet, 1931; Devesa; Kazmi, 1964; McCarty; Moore & Mulligan, 1956). Kazmi (1964) listed crosses between *C. acanthoides* and 14 other species and between *C. nutans* and four others.

Moore & Mulligan's (1959) study of hybridization between *C. nutans* and *C. acanthoides* (= *C.* × *orthocephalus* Wallr.) showed that several morphologically intermediate plants had chromosome numbers ($2n$ = 17, 18, 19, 21) intermediate between those of the parental species. They also noted a strong correlation between morphology and chromosome number (i.e., the more closely a hybrid approached the morphology of one of the parental types the more likely it was to have a chromosome number either close to or the same as that parent). A few hybrid plants had chromosome numbers of $2n$ = 16, but the majority of the hybrids had chromosome numbers of $2n$ = 22, which led Moore & Mulligan to hypothesize that backcrossing to both parents had occurred to produce the chromosome numbers of the parental stock. Of the carpellate parents with a known chromosome number of $2n$ = 22, 23 of the 24 hybrid progeny examined had $2n$ = 22.

Wagner reported the alkaloids acanthoine and acanthoidine for *Carduus acanthoides* and referred readers to Bohlmann *et al.* for a list of polyacetylenes. No sesquiterpene lactones were noted by Seaman for *Carduus,* but Abdel-Salam isolated an unusual triterpene ester from *C. getulus* Pomel. Amer and colleagues' report of flavonoids from *C. pycnocephalus* appears to be one of the few reports of flavonoids isolated from *Carduus.*

There are no economically important members of this group.

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3. **Silybum** Adanson, Fam. Pl. **2:** 116, 605. 1763, nom. cons.

Annual or biennial herbs. Stems 20–150 cm tall, simple or sparingly branched, robust, glabrous or slightly tomentose, lacking wings. Leaves near base of stem petiolate, upper cauline leaves sessile and auriculate-clasping; blades to 80 cm long and nearly 40 cm wide, broadly lanceolate to oblanceolate, lower leaves deeply but irregularly lobed, upper leaves entire or shallowly lobed, white veined or variegated, glabrescent to puberulent; margins spiny. Capitula 3–6 cm wide, homogamous, discoid, solitary at the ends of branches. Involucre hemispheric to ovoid; bracts imbricate, multiseriate, the outer ones with a broad, firm, spinulose-ciliate base and a coriaceous, subfoliose, strongly reflexed, spine-tipped and basally spine-margined appendage, inner bracts lanceolate, erect and unappendaged. Receptacle flat to slightly convex, densely bristly. Flowers perfect. Corolla slightly zygomorphic, purplish; tube narrow, elongate, glabrous to puberulent, throat short, abruptly expanded, unequally divided by the sinuses of the long, linear, acute lobes. Staminal filaments glabrous, connate below; anthers shortly tailed at base, apical appendage firm, triangular, glabrous. Style smooth below a distinct collar of hairs at base of the elongate, papillose, connate branches. Achenes basifixed, obovoid-oblong, 6–7 mm long, somewhat compressed, glabrous, black or brown with lighter streaks, with a distinct annular rim subtending the pappus. Pappus in several series, outer setae white, minutely barbellate, innermost bristles considerably shorter, capillaceous, basally connate and deciduous as unit. Base chromosome number 17. TYPE SPECIES: *Carduus Marianus* L. = *Silybum Marianum* (L.) Gaertner, type cons. (Name the Latin one for the milk-thistle, from the Greek name *sillybos* or *silybon.*)—MILK-THISTLE.

A genus of two species, *Silybum Marianum* (*Mariana Mariana* (L.) Hill) and *S. eburneum* Coss. & Dur., both native to the Mediterranean area, the former now widespread in North and South America. *Silybum Marianum,* milk-thistle, $2n = 34$, is naturalized locally in many parts of the United States, particularly in drier waste areas, along roadsides, and in disturbed pastures. In the Southeast it is rare and may be little more than a waif locally escaped from cultivation. Small (1933) reported it south to Alabama; Cory listed it west to Texas; yet it was not treated by either Correll & Johnston or Barkley). Johnson (1978) recorded it from Goochland County, Virginia; Thieret (1968) reported it as new to Louisiana, and E. B. Smith (1988) noted it as a local escape from cultivation in three widely separated localities in Arkansas. This species has become a common and troublesome weed in the pampas of Argentina (Mabberly) and in areas with a Mediterranean climate along the Pacific coast of North America (Howell, Munz), where a seed weevil, *Rhinocyllus conicus,* (Hawkes *et al.,* 1972) has been released to control it.

Silybum Marianum was treated as a species of *Carduus* by Linnaeus and was initially given generic status as *Mariana* by Hill. Shortly afterward Adanson proposed the now conserved name *Silybum* for the same taxon. Cassini grouped *Silybum* with *Alfredia* Cass. (= *Carduus* subgenus *Alfredia* (Cass.) Kazmi) and *Echenais* Cass. (treated as *Carduus* by Lessing, *Cnicus* by Bentham) as an unspecified division of the Carduinae. Lessing placed *Silybum* with *Tyrimnus* Cass. and *Galactites* Moench in an unranked division, *Silybeae,* of the subtribe Carduinae, on the basis of their monadelphous filaments, multiseriate pappus, and compressed, glabrous achenes. The same genera were recognized as subtribe *Silybeae* by De Candolle. A detailed study of seed anatomy and morphology led Dittrich (1970, 1977) to group *Silybum* informally with *Carduus, Cirsium,* and *Modestia* Charadze & Tamamshiam, while *Galactites* and *Tyrimnus* were aligned with *Picnomon* Adanson and *Jurinea* Cass.

Silybum is distinguished from *Galactites, Cirsium,* and *Modestia* by its simple or barbellate (not plumose) pappus bristles. It differs from *Tyrimnus* and *Carduus* in its uniseriate pappus and mottled cauline leaves that are markedly different from the reduced leaves that subtend individual heads. In addition, *Silybum* is distinguished from other genera of Cardueae of the Southeast by its connate staminal filaments.

Chromosome counts of $2n = 34$ have been reported for *Silybum Marianum* (Goldblatt, 1981; Heiser & Whittaker; Larsen). Moore & Frankton (1962) found that the chromosomes of *Silybum* are somewhat shorter than those of *Cirsium* but are similar in width and appearance. They also noted that the thickness of the chromosomes and the total amount of chromatin in the nucleus are similar in species of *Silybum, Carduus, Cirsium, Cnicus,* and *Onopordum.*

Wagner reported that flavanones and flavonols were restricted to *Silybum, Centaurea,* and *Carthamus.* Both species of *Silybum* were noted as exceptional for their production of flavonolignans, compounds known from only one other genus, *Hydnocarpus* (Flacourtiaceae). Flavonoids isolated from *Silybum* include silybin, silydianin, silychristin, and silymarin (Wagner *et al.,* 1971; Wagner, 1977; Cappelletti & Caniato, 1983, 1984; Belikov, 1985; Hassan, 1985). The antihepatotoxic activity of the flavonolignans has been of considerable

interest for medicinal purposes (Hahn *et al.*; Sharma & Singh; Schrall & Becker; Fiebig & Wagner; Hikino *et al.*; Wagner, 1986). Mabberley noted that the antihepatotoxic qualities of *S. Marianum* have been known since the time of Dioscorides and that they are now known to work as effective antidotes for *Amanita* poisoning, since they are able to displace phalloidin from membrane receptors. In addition, the alkaloids tyramine and histamine have been isolated from *Silybum* (see Wagner, 1977, for references).

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4. **Onopordum** Linnaeus, Sp. Pl. **2:** 827. 1753; Gen. Pl. ed. 5. 359. 1754.

Biennial herbs. Stems stout [very short], fistulose, much branched, spiny winged, densely tomentose, rarely glandular. Leaves near base of stem petiolate, middle to upper cauline leaves sessile, semi-auriculate, clasping; blades lanceolate to oblanceolate, toothed to pinnatifid [pinnatisect], glabrescent to arachnoid-tomentose; margins spiny. Capitula homogamous, discoid, terminal or axillary, solitary to corymbosely arranged, peduncles usually prickly winged.

Involucre hemispherical to globose [glabrescent or] arachnoid-tomentose; bracts imbricate in several series, narrowly lanceolate [oblanceolate], coriaceous, spine tipped, the margins scabrous; outer bracts commonly triangular, erect to recurved, adpressed to lax; inner bracts narrowly lanceolate, glabrescent. Receptacle flat to slightly convex, glabrous, fleshy, alveolate with short, basally fused scales along the margins of the pits, but never densely bristly. Flowers perfect, homogamous, actinomorphic to slightly zygomorphic. Corollas lilac to purplish, glabrous or with scattered sessile glands; tube slender, elongate, throat short, slightly expanded, actinomorphic or saccate and unequally divided by the sinuses of the linear, elongate lobes. Staminal filaments glabrous, attached at base of corolla throat; anthers sagittate, with narrow, acuminate, apical appendages often extending beyond corolla lobes. Style smooth or rugose below a distinct collar of hairs at base of the papillate, connate to slightly divergent branches. Achenes basifixed, 4–5 mm long, tetragonal, commonly laterally compressed, brown, rugulose, glabrous. Pappus bristles multiseriate, unequal, capillary or barbellate [plumose], often flattened, basally connate, deciduous as unit. Base chromosome number 17. LECTOTYPE SPECIES: *Onopordum Acanthium* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada **3:** 556. 1913; also, Hitchcock & Green, Nom. Prop. Brit. Bot. 179. 1929; Jackson, Index Linn. Herb. 109. 1912. (Name Latinized from the ancient Greek name of the plant, *Onopordon,* from *onos,* donkey, and, *porde,* flatulence. Pliny stated that it caused flatulence in donkeys.)—SCOTCH THISTLE, COTTON THISTLE.

A genus of about 40 species of Mediterranean Europe and Western Asia. *Onopordum Acanthium* is naturalized in various parts of the world. *Onopordum* is distinguished from other thistles by the absence of bristles or paleae on the receptacle. The genus appears to be closely related to the large genus *Cousinia* Cass. and more remotely to *Jurinea* Cass. and *Saussurea* DC. *Onopordum Acanthium* is often found escaped from cultivation, established along roadsides, in dry, waste areas, and in disturbed pastures. It is the only species of this genus reported from the Southeast (Small, 1933; Cronquist, 1980), but it does not appear in the *Flora of the Carolinas* (Radford, *et al.*). McGregor reported *O. Acanthium* as a serious weed of infrequent, localized occurrence and often found in feedlots; Johnson (1974) noted only two collections from Virginia. Among *Onopordum* species, it can be distinguished by its large seeds and numerous slender, reflexed, involucral bracts (± 2 mm wide at the base).

Nearly 100 years have passed since the last revisionary treatment of the genus was published by Rouy, who recognized 24 species in three sections (*Acaulia* Rouy, *Erecta* Rouy, *Reflexa* Rouy) based on characters of habit, involucral bracts, and pappus. Rouy placed *Onopordum Acanthium* in sect. *Reflexa* (now ONOPORDUM), which was characterized by erect, winged stems, recurved involucral bracts, and scabrous or semi-plumose pappus bristles. Franco established the monotypic subgenus ACAULON and recognized four sections (ONOPORDUM, ERECTA, ECHINATA Franco, RECURVATA Franco) under subg. ONOPORDUM. The monotypic sect. ONOPORDUM was differentiated by its lanate or tomentose pubescence of unicellular hairs; lack of reticulate veins on

the lower side of the leaves; linear-subulate, erecto-patent involucral bracts shorter than the flowers; eglandular corolla lobes; and scabrid pappus hairs.

A base chromosome number of 17 was indicated by Moore & Frankton's (1962) report of the chromosome number $2n = 34$ for *O. Acanthium* (see also Poddubnaja-Arnoldi and Morton, among others), *O. illyricum* L., and *O. Sibthorpianum* Boiss. & Heldr. All subsequent chromosome counts for species of *Onopordum* have been $2n = 34$ or $n = 17$ (see Moore, 1973; Goldblatt, 1981, 1984, 1985, for references). Moore & Frankton (1962) noted that the chromosome number and morphology of *Onopordum* are indistinguishable from those of *Cirsium.*

Relatively few phytochemical studies have been undertaken on *Onopordum.* The phenolic compound cynarin was reported from *O. illyricum,* and the alkaloids choline and stachydrine were reported from *O. Acanthium* (see Wagner for references). The sesquiterpene lactone onopordopicrin has been isolated from *O. Acanthium, O. leptolepis* DC., *O. tauricum* Willd., and two costunolide and melitensin sesquiterpene lactones were reported from *O. leptolepis* DC. (see Seaman for references). Rustaiyan *et al.* have isolated onopordopicrin and two related esters, eudesmanolides, and eudesmane derivatives from *O. carmanicum* (Bornm.) Bornm. Rustaiyan *et al.* reported that the 15-hydroxyl germacranolide with an 8-alpha-acyloxy group isolated from *O. carmanicum* is known from *Jurinea* (Hermout & Šorm) and that similar sesquiterpene lactones have been reported from *Centaurea, Arctium,* and *Cnicus* species, as well as from *Dicoma* Cass., of the Mutisieae.

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5. **Arctium** Linnaeus, Sp. Pl. **2:** 816. 1753; Gen. Pl. ed. 5. 357. 1754.

Biennial herbs. Stems erect, striate, branching, glabrous to less often arachnoid-hairy; taproots stout, elongate. Leaves petiolate, petioles solid or fistulose; blades ovate to ovate-oblong, obtuse to cordate based, the upper surface with scattered sessile glands, the lower surface commonly arachnoid-hairy and glandular, the glands numerous, sessile; blade margins entire to serrate or rarely laciniate, often remotely dentate. Capitula homogamous, discoid, ca. 2–5 cm wide, borne in several- to many-headed racemes or cymes. Involucre subglobose, green [rarely purple], glabrous [or with arachnoid indumentum], bracts multiseriate, imbricate, narrowly lanceolate, subequal, coriaceous, basally appressed and slightly keeled, apices subulate, inwardly hooked, and on the outer bracts strongly reflexed. Receptacle flat, with numerous, white, subulate, scabrous scales. Flowers perfect, actinomorphic, corollas lavender to purple (rarely white), glabrous, tube narrow, equal to or slightly longer than the slightly expanded throat and acute to acuminate, elongate, glabrous lobes. Staminal filaments glabrous, anthers stramineous, sagittate, apical appendages with mucronate tips. Style slightly swollen at base, smooth below an indistinct collar of hairs found at the base of papillate, cuneate branches. Achenes basally attached, 4–7 mm long, oblong, somewhat compressed, apically truncate, commonly rugose, glabrous, many nerved, light to dark brown, often mottled. Pappus bristles numerous, unequal, relatively short (ca. 2 mm long), barbellate, individually and readily deciduous. LECTOTYPE SPECIES: *Arctium Lappa* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada **3:** 547. 1913; also see Hitchcock & Green, Nom. Prop. Brit. Bot. 179. 1929. (Name from Greek, *arction,* a plant name from *arctos,* a bear, because of the rough involucre; cf. Munz.)—BURDOCK.

A Eurasian genus of about ten species, some of which are widely naturalized in southern Europe and Asia Minor, China(?), Japan, and North America. Three introduced species, *A. Lappa* L., great burdock; *A. minus* (Hill) Bernh., common burdock; and *A. tomentosum* Miller, woolly burdock, are known from the southeastern United States.

Perring recognized five species in Europe and, in the following quote, clearly stated the difficulties encountered in the taxonomy of the genus. "Specific limits within this genus cannot be clearly defined, each species showing great variation in hairiness of leaves and capitula, length of peduncles and colour of capitula and florets. All taxa are interfertile and although they are normally autogamous, outbreeding sometimes occurs. This has resulted in innumerable intermediates which are fully fertile and breed true from seed."

Four species (*Arctium Lappa, A. nemorosum* Lejeune & Courtois, *A. to-*

mentosum, and *A. minus*) based on characteristics of the achenes, corollas, involucral bracts, leaves and arrangement of the inflorescence were recognized by Fernald & Wiegand, but they were uncertain of the role hybridization had played among the taxa found in America. Arènes (1950) recognized four species (*A. Lappa, A. minus, A. tomentosum,* and *A. Chabertii*) and two sections, *Eglandulosa* (i.e., ARCTIUM including *A. Lappa* and *A. minus*) and GLANDULOSA. Each species was subdivided into various taxa. In addition, Arènes (1950) recognized nine interspecific hybrids involving *A. Lappa* or *A. minus,* two of which (*A.* ×*mixtum* Nym., *A.* ×*nothum* (Ruhm.) Weiss) were said to occur in North America (Moore & Frankton, 1974; Gross *et al.*). The division between glandular and eglandular taxa set forth by Arènes was considered to be a seemingly natural separation by Moore & Frankton. Cronquist (1980) notes that *A. nemorosum* may also be of hybrid origin.

The three species in the Southeast are found in waste places, along roadsides and streambanks, and in overgrazed pastures. As Gross *et al.* noted, the biennial habit of these species confines them to areas not cultivated or otherwise disturbed on an annual basis. Wiegand & Eames found that *A. minus* and *A. Lappa* are common in both rich soil and clay. Rollo *et al.* reported a strong overlap in distribution between *A. minus* and *A. Lappa* in their study area. All three are common in the Northeast, but only *A. minus* occurs with any regularity south of the Carolinas. Throughout its range in the Southeast it is more likely to be found in the mountains than in the Piedmont.

Mulligan & Kevan described *Arctium minus* as an autogamous biennial weed that is frequently visited by insects, despite the lack of any noticeable odor. These findings corroborated the work of Mulligan & Findlay, who noted that *A. minus* set viable seed even when covered with a "pollination bag." Gross & Werner reported that *A. minus,* which reproduces only by seed, will not flower in the second year if conditions are poor. Gross & Werner also determined that the probabilities of a rosette's flowering in a given year are linked to rosette size, but that rosette size is not linked to age. Total achene (hence seed) production was shown to be correlated with either rosette size or the height of the flowering stem, yet differences in total fruit production were shown to be a function of the number of capitula on a plant. No relationship was found between rosette size and the number of fruits in a capitulum (Gross & Werner).

Hawthorn & Hayne discovered that the mean number of fruits per plant in *A. minus* (13,400) was significantly greater than in *A. Lappa* (8200), as were the mean numbers of heads per plant (338 versus 112, respectively). Predispersal seed predation by the microlepidopteran *Metzneria lappella* accounted for the loss of 28 to 71 percent of the achenes of *A. minus* but only 15.5 percent of those of *A. Lappa.* Hawthorn & Hayne also found that only about one fifth of the heads of *A. minus* were shed during the winter compared to 62 percent of the heads of *A. Lappa.* This pattern of herbivory, along with the observation that very few achenes are dispersed from heads of *A. minus* because of the contraction of the involucre led Hawthorn & Hayne to conclude that *A. Lappa* is more efficient than *A. minus* in seed dispersal.

Rollo *et al.* observed four biotypes of *Arctium* present in their study popu-

lations. These biotypes, including the two parental species (*A. minus* and *A. Lappa*), were differentiated on the basis of size of capitula, length of peduncles, stem color, involucral characters, degree of insect herbivory, and allometric measurements. The relative abundance of these biotypes changed yearly. A "scenario" involving differential insect predation, hybrid inferiority, and differential dispersal was suggested to explain the dynamics of burdock populations. In accord with the study by Hawthorn & Hayne, Rollo *et al.* noted that the capitula of *A. minus* remain tightly closed allowing few achenes to fall out, while the capitula of *A. Lappa* open widely, allowing many achenes to fall beneath the parent plant. In addition, Rollo *et al.* observed that *A. minus* is more likely to colonize new, disturbed habitats than is *A. Lappa*, suggesting that this was due to the tightly closed capitula of *A. minus* that are not so readily deciduous as those of *A. Lappa*. They concluded that the capitula of *A. minus* are more suited to dispersal by animals to which they are readily attached by their hooked involucral bracts. Noting common burdock's extremely high seed mortality from the moth *Metzneria lappella*, Rollo *et al.* characterized *A. minus* as a fugitive species that depends on long-distance dispersal by animals to escape moth predation in both time and space.

On the basis of counts of $n = 18$ (Nakajima), $2n = 36$ (Tarnavschi) and $2n = 32$ (Sugiura) for *A. Lappa*; $2n = 36$ (Löve & Löve, 1944; Tarnavschi) for *A. nemorosum*; $2n = 36$ (Tarnavschi) and $2n = 32$ (Wulff) for *A. minus*; and $2n = 36$ for *A. tomentosum* (Poddubnaja-Arnoldi; Tarnavschi), Löve & Löve (1961) considered *Arctium* to have a basic chromosome number of nine. Mulligan has since reported $2n = 36$ for *A. minus*.

Despite many claims of hybridization between species of *Arctium* (Arènes, 1950; Moore & Frankton, 1974; Weigand & Eames), only one study has directly addressed this subject. Rollo *et al.* studied the allometric and electrophoretic variation between four biotypes representing two parental types (*A. minus, A. Lappa*) and two putative hybrids. They concluded that three of the four biotypes could be clearly distinguished by allometric measurements. Electrophoretic patterns showed unique isozymes in both parental biotypes which also differed from one another to the greatest extent allometrically. The putative hybrid biotypes were found to share various isozymes from the two parental types, thus supporting the hypothesis that these biotypes were hybrids.

The sesquiterpene lactone arctiopicrin was found in *Arctium minus, A. Lappa, A. nemorosum,* and *A. tomentosum* and onopordopicrin was isolated from *A. minus* (see Seaman for sources). In addition, the triterpenes β-eudesmol, arctiol, eremophilene petsitolone, and fucinanolide were reported for *A. Lappa* (see Wagner, 1977, for sources). Wagner (1977) reported the flavonoids isoquercitin, astragalin, quercetin 3-O-arabinoside, quercimeritrin, rutin, and kaempferol 3-O-rhamnoglucoside from *A. minus*. Alkaloids of unknown structure have also been reported for *A. Lappa* and three other unnamed species of *Arctium* (Wagner, 1977).

Some of the many economic uses of *Arctium* that have been well documented by Moore & Frankton (1974) include root extracts used as laxatives, diuretics, sudorifics, blood purifiers, and hair restorers, as well as constituents in "wood tea" and as an emergency coffee substitute (Hegi, 1929; Youngken, 1948).

Moore & Frankton also cited Rousseau & Raymond's report that the young leaves and dried roots were eaten by the American Indians until fairly recently, and Yanovsky's record that *A. Lappa* was eaten as greens and the roots were cooked for soup and dried and stored for winter food. *Arctium Lappa* is cultivated for its edible roots (*gobo*) in Japan, and the young leaves are used in salads in both Japan and Scandinavia (Mabberley). The hooked involucral bracts of *Arctium* were the inspiration for the now widely used "Velcro" fabric closures.

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6. **Centaurea** Linnaeus, Sp. Pl. **2**: 909. 1753; Gen. Pl. ed. 5. 389. 1754.

Annual to perennial herbs [rarely dwarf shrubs with spiny branches or larger evergreen shrubs]. Stems tomentose or scabrous to hirsute with multicellular hairs, rarely glabrous, commonly with sessile glands. Leaves sessile to (less often) petiolate, alternate or all basal; blades narrowly lanceolate to ovate, entire to pinnatifid; margins scarcely or not at all prickly. Capitula heterogamous, discoid or falsely radiate, hemispherical to subglobose, terminal or axillary, commonly solitary or in loose cymose clusters, subsessile to long pedunculate. Involucre ovoid, subglobose [nearly cylindrical, oblong or fusiform], commonly contracted apically, bracts imbricate in several series, often striate, glabrous to tomentose, either shortly spine tipped or more commonly with an orbicular, lanceolate or triangular, scarious or hyaline, erose to pectinate appendage, or occasionally the appendage absent and the apical margin merely pectinate or lacerate. Receptacle flat to slightly convex, with numerous smooth, white bristles. Florets perfect or sterile. Corollas lavender, blue, yellow, or white; marginal florets sterile [perfect], occasionally with an irregularly expanded, falsely radiate corolla; inner florets perfect, discoid, actinomorphic, tube often elongate, slender, throat expanded, lobes long, linear to lanceolate. Staminal filaments glabrous; anthers stramineous or commonly the same color as corolla, tailed at base, though often shortly, the apical appendage narrow, acute. Styles smooth

below a distinct collar of hairs at base of the short, slightly divergent, narrowly truncate to acute, papillate branches. Achenes obliquely or laterally attached to receptacle, oblong or ovoid, compressed or obtusely 4-angled, seldom evidently nerved, glabrous at maturity. Pappus of several series of unequal scabrous or barbellate [plumose] bristles or narrow scales, often much reduced, or absent. LECTOTYPE SPECIES: *Centaurea Centaurium* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2. **3:** 556. 1913; also, R. McVaugh, Fl. Novo-Galiciana, 209. 1982. (Name from Greek, of the centaurs, who were said to have used it in healing.)—KNAPWEED, STAR-THISTLE.

A genus first proposed by Linnaeus for 50 species, *Centaurea* currently is comprised of some 450 (Mabberley) to 600 species (Holub, 1972a; Wagenitz, 1985a). Various members of this genus have become widespread throughout the world, but species diversity is concentrated in the Mediterranean and Near Eastern regions. Dostál (1976) included 221 species in his treatment of *Centaurea* for the *Flora Europaea,* and Wagenitz recognized 172 in the *Flora of Turkey* (1975) and 89 in *Flora Iranica* (1980). Wagenitz (1985a) indicated that 260 species in 38 sections are known from Southwest Asia, with the greatest numbers in southern and eastern Turkey and adjacent Iran and Iraq. In this area, there are several widespread species, as well as 201 endemics, many of which occupy restricted areas. The large number of endemics and the coherent distribution of most groups (often delimited as subgenera, sections or, in some cases, genera) led Wagenitz (1985a) to conclude that speciation has occurred in relatively recent times and *in situ.* Further, Wagenitz believed that the diversity of the group can only be understood by taking into account the capitulum which, according to both Wagenitz and Burtt, functions as a single flower and its fruit might in other families. To illustrate this point, Wagenitz noted the wide range in the number of flowers per capitulum in different species (4 or 5 in *C. virgata* Lam. to over 200 in *C. macrocephala* (Muss.) Puschk. ex Willd.), as well as several forms of dispersal: a well-developed pappus as a means of wind dispersal (anemochory); small, deciduous capitula with hooked appendages suited for animal dispersal of whole capitula (epizoochory); and an elaisome that mediates dispersal by ants (myrmecochory). (See also Dittrich, 1968a, b.)

Only two species are indigenous in the United States: *Centaurea americana* Nutt., which enters the Southeast in western and southwestern Arkansas (E. B. Smith, 1988) and western Louisiana, and *C. Rothrockii* Greenman, a species of the Great Plains. However, nearly twenty other species have become established in parts of the United States, some as pernicious weeds.

Species of *Centaurea* in the southeastern United States are most often found in disturbed fields, waste places, and along roadsides. Cronquist (1980) recognized eight species in the Southeast, but several taxa (*C. dubia* Suter., *C. nigra* L., *C. Jacea* L., *C. Calcitrapa* L.) that he treated occur, if at all, only sporadically along the northern boundaries of this region. Three of these species (*C. dubia, C. Jacea, C. nigra*) are perennials that are widespread in the Northeast. They are distinguished from other taxa of *Centaurea* in the Southeast and from each other by leaf characters and subtle distinctions of the involucral bract appendages (Cronquist, 1980, among others).

The dubious occurrence of various taxa is reflected in Johnson's inclusion (see distribution maps in Harvill *et al.*) of *C. Calcitrapa, C. dubia, C. nigrescens* Willd., and *C.* ×*pratensis* Thuill. (*C. Jacea* × *C. nigra*), which are not treated by Ahles in Radford *et al.* Small (1933) considered only *C. solstitialis* L., *C. melitensis* L., and *C. Calcitrapa* to be naturalized and *C. Cyanus* L. to have escaped from cultivation in the Southeast.

Centaurea Cyanus, bachelor's-button or cornflower, is a widely cultivated winter annual that is periodically found to be well established in fields and waste places and along roads. It is distinguished by its narrow, nearly linear leaves and heads with an outer series of elongate, zygomorphic flowers, the corollas of which are usually bright blue (or occasionally pink or white).

Centaurea maculosa Lam., spotted knapweed, a short-lived perennial that has become one of the most serious weeds of western rangelands (Boggs & Story), is commonly encountered in old fields and pastures and along roadsides in the Southeast. Although similar to *C. Cyanus* in having an outer series of elongate, expanded florets, *C. maculosa* differs in its pinnatifid leaves and lavender flowers.

As noted by Cronquist (1980), *C. melitensis,* a yellow-flowered European species similar in many respects to *C. solstitialis* (also yellow flowered), is found only occasionally in South Carolina and Georgia. *Centaurea solstitialis,* a widespread and pernicious weed in several western states, is not well established in the Southeast. *Centaurea Calcitrapa,* another uncommon introduction to this region, can be differentiated from *C. solstitialis* by its purple florets, wingless stems, and epappose achenes. Both of these species are readily differentiated from others of *Centaurea* by their strongly spiny involucral bracts.

Centaurea americana, an annual plant common in grasslands in the Great Plains and most readily distinguished by its large, unarmed heads and well-developed pappus, enters the Southeast along the eastern border of its range which extends from Missouri southward through western Arkansas and the border of Louisiana with Texas, as noted above.

From the time of Cassini to the present, the question of generic boundaries in the subtribe Centaureinae and related subgeneric groupings within *Centaurea sensu lato* has generated considerable controversy. The rather lengthy account that follows outlines a part of the difficulty and complexity of the group.

Early in his serial publications on the Compositae in the *Dictionnaire des Sciences Naturelles,* Cassini (1817) recognized the tribes Cardueae (as "Carduacées") and Centaureeae (as "Centauriées"), both names invalidly published, to which he attributed 17 and 11 genera, respectively. Later (1819), he validated these and other tribes with Latin names. By 1830, when he completed his treatment for publication, Cassini had come to recognize in the Centaureeae 41 genera, nearly 30 of which he described himself. He aligned the Centaureeae with the Cardueae and Carlineae, but considered the possibility of recognizing the Cardueae and Centaureeae as subtribes of a single tribe, Cardueae. Initially, Cassini had differentiated Centaureeae from Cardueae by characteristics of the anther appendages (apically fused and curved, not straight as in the Cardueae), achene, and pappus. He noted that while both the Centaureeae and Cardueae have laterally compressed, obovate achenes with four more or less pronounced

sides or ribs, the basal areole ("l'aréole basilaire") or point of attachment of the achene of the Cardueae is sessile, broad ("large"), smooth ("plane"), curved ("arrondie"), slightly oblique ("un peu oblique-antérieure"), and lacking a rim or margin. The Centaureeae, on the other hand, were reported to have sessile, very oblique basal areoles strongly adherent to the receptacle ("la substance du clinanthe") and situated in a broad, diamond-shaped notch with curvilinear sides ("une large échancrure en losange, à bords curvilignes").

As Cassini observed, the pappus of the Centaureeae is considered to be double or two ranked. The outer rank is comprised of several series of imbricate squamellae, the outermost of which are extremely short, flattened, obtuse, and barbellate. There is a gradual transition from the outer squamellae to an inner series of longer, cylindrical, bristle-like setae. A single series of very short, membranaceous, truncate squamellae constitutes the innermost rank of the double pappus. The pappus of the Cardueae is comprised of numerous series of unequal barbellate setae; the outermost series is composed of very short, filiform bristles, while the inner series is of barbellate setae flattened at the base, triangular ("triquètres") in the mid part, and filiform near the apex. In later descriptions, Cassini (1830) noted the outwardly curved corollas and outer series of sterile flowers in the Centaureeae (absent in the Cardueae) and the unique zygomorphic nature of the corollas in the Cardueae as differentiating characters. These distinctions, which have been the foundation for many subsequent classifications, were used by Dittrich (1977).

Lessing placed in synonymy under *Centaurea* nearly 30 genera that Cassini had described. Until recently, Lessing's concept of the tribe and of *Centaurea* has been followed by most workers.

Spach's tribal arrangement, patterned on Cassini's, included many of the characters Cassini used to delimit the tribes. Spach's proposed classification of *Centaurea* included 27 subgenera, six of which (*Chartolepis* Cass., *Jacea* Miller, *Cyanus* (Miller) Pers., *Lopholoma* Cass., *Hymenocentron* Cass., *Calcitrapa* (Heist ex Fabr.) Pers.) he treated in detail. Although he utilized suites of characters from the flowering capitula in his descriptions, differences in the involucral bracts were stressed in his segregation of these six taxa.

Bentham followed Lessing's tribal treatment in many respects but returned the Arctoteae and Calenduleae to tribal status. The subtribe Centaureinae comprised ten genera in Bentham's treatment. *Centaurea* was divided into 22 series ("vix Sectiones") most of which were based on Cassini's genera.

The first infrageneric treatment for *Centaurea* was put forth by A. P. de Candolle in the third edition of Lamarck & De Candolle's *Flore Française* (1805). Six sections were proposed by De Candolle (see Brizicky) as reductions of Jussieu's generic concepts: *Centaurea* (involucral bracts entire, foliaceous, not spinose), *Rhaponticum* (Ludwig) DC. (involucral scales scarious, not ciliate or spinose), *Cyanus* (Miller) DC. (involucral scales ciliate, not spinose), *Seridia* (Juss.) DC. (involucral scales terminated with numerous prickles disposed like fingers of the hand), *Calcitrapa* (Heist. ex Fabr.) DC. (involucral scales terminated by one spine that is laterally divided towards the base), and *Crocodylium* (Hill) DC. (involucral scales terminated by a simple spine).

Shortly afterward, Persoon (1807) proposed ten subgenera for *Centaurea*

(*Amberboa* Pers., *Phrygia* Pers., *Cyanus* (Miller) Pers., *Jacea* (Miller) Pers., *Stoebe* (L.) Pers., *Calcitrapa* (Heist. ex Fabr.) Pers., *Seridia* (Juss.) Pers., *Crocodylium* (Hill) Pers., *Verutum* Pers., and *Crupina* Pers.) based primarily on involucral bract characters similar to those used by De Candolle in his sectional treatment.

In the year that Cassini finished his series of articles for Cuvier's *Dictionnaire des Sciences Naturelles,* George Don (1830) put forth a classification with six sections, including five of those proposed by De Candolle (*Centaurea, Cyanus, Calcitrapa, Seridia, Crocodylium*). Don described the section *Crupina* (involucral scales entire), as well as subsections for most of the other sections included in his treatment.

De Candolle's treatment in his *Prodromus* (1837) divided *Centaurea* into five series and 31 sections. Article 33.4 of the International Code of Botanical Nomenclature rules that De Candolle's sections and series were invalidly published because of their inverted order (i.e., sections as subdivisions of series). As with his earlier sectional treatment (see above), De Candolle relied on characters of the involucre to differentiate his series, but expanded his delimitation of sections to include characteristics of the involucre, flowers, achenes, and pappus. The majority of the sections recognized by De Candolle were originally described by Cassini as genera.

De Candolle's inclusive treatment was followed by many subsequent workers, including Bentham (see above) and Hoffmann. Utilizing characters of the involucre and pappus, Hoffmann recognized in *Centaurea* 41 sections, many of which were based on Cassini's genera. Several of De Candolle's sections were treated as genera by Boissier (e.g., *Aetheopappus* Cass., *Psephellus* Cass., *Phaeopappus* (DC.) Boiss.), who also recognized as genera groups treated as infrageneric categories by other workers (e.g., *Stizolophus* Cass., *Acroptilon* Cass., *Melanoloma* Cass.). Boissier distinguished 16 sections in *Centaurea.*

Hayek's (1901) classification comprised nine subgenera (*Centaurium, Microlophus* (DC.) Hayek, *Calcitrapa, Cyanus, Jacea, Odontolophus* (Cass.) Hayek, *Crocodylium, Cheirolophus* (Cass.) Hayek, *Plectocephalus* Hayek) and 18 sections (mostly in the subgenera *Calcitrapa, Cyanus,* and *Jacea*) in a well-documented treatment of *Centaurea* in Austria-Hungary. Hayek proposed five new sections (*Eucalcitrapa* (subg. *Calcitrapa*), *Eucyanus* and *Pannophyllum* (subg. *Cyanus*), *Eujacea* (subg. *Jacea*), *Eucheirolophus* (subg. *Cheirolophus*)) differentiated, for the most part, by characteristics of the involucral bract appendages.[4]

More recently, still other systems have been presented in anatomical, palynological, cytological, and floristic studies. Wagenitz's (1955) work on the pollen morphology and systematics of *Centaurea* has been used by subsequent workers as a basis for various systematic schemes (e.g., Dostál, 1973; Dittrich, 1977; Guinochet; Guinochet & Foissac). Wagenitz recognized eight pollen types (*Serratula, Centaurium, Crupina, Scabiosa, Dealbata, Jacea, Montana, Cyanus*) in *Centaurea sensu lato* based on differences in size and shape of the grains and the sculpturing and structure of the exine. His data came from about 26

[4]The use of the prefix "Eu-" is specifically ruled against in Article 21.3 of the International Code.

sections of *Centaurea* and from 16 closely related genera. Wagenitz's observations have been elaborated on by Štepa (1959, 1960) and Velari. Velari noted, in confirmation of Wagenitz, that *Centaurea* presented solitary, isopolar and radiosymmetric pollen grains, the shape of which varied from suboblate to euprolate. In addition, the grains were reported to be tricolporate with operculate apertures, and the sculpturing was described as echinate, echinulate, or verrucate.

Dittrich (1968a, b) studied in considerable detail the morphology and anatomy of achenes from eleven genera and in *Centaurea* from nearly 25 sections. He concluded that the form of the hilum (basal, lateral, or caudate), the mechanisms for fruit detachment (the elaiosomes or simple parenchymatic tissues), achene pubescence, and the consistency of the pericarp are important for the determination of generic boundaries in the Centaureinae. While considerable variation can be noted in pappus characters of taxa in the Centaureinae, Dittrich proposed a new definition of single and double pappus in this group and concluded that this character is of limited value for defining genera in this subtribe.

Dittrich (1977) recognized 27 genera in the subtribe Centaureinae. In a manner very similar to that of Cassini, he characterized the group by the concave and lateral-adaxial orientation of the detachment area of their fruits and their "double pappus" comprised of an outer rank of bristles or scales elongated from outside to inside and an internal rank often different from the outer.

Utilizing Wagenitz's (1955) seven basic pollen types as the groundwork for his "inner taxonomy," Dostál (1973) resurrected numerous old generic names, elevated several sections of *Centaurea* to generic rank and described a new genus, *Wagenitzia* Dostál. This resulted in the recognition of approximately 50 segregates from *Centaurea sensu lato*. Combinations in several of the genera recognized by Dostál were made by both Holub (1972b) (*Acosta* Adanson, *Colymbada* Hill emend. Holub, *Cyanus* Miller, *Jacea* Miller) and Sojak (*Cyanus, Jacea, Calcitrapa* Heister ex Fabr., *Xanthopsis* (DC.) Koch, *Heterolophus* Cass., *Acosta*; lectotypes were provided for *Behen* Hill, *Psora* Hill, and *Sagmen* Hill). The lack of detailed knowledge of the western Asiatic and Mediterranean groups led Dostál (1975) to reconsider making the numerous nomenclatural combinations necessary if these segregates are recognized as genera as he had earlier proposed (Dostál, 1973). Instead, his account for the *Flora Europaea* (Dostál, 1976) treated *Centaurea* as comprising 12 subgenera and 26 sections.[5]

Jeffrey (1968) listed 59 genera of the Centaureeae from the most "Mutisioid"

[5]The combination subgenus *Microlophus* (Cass.) Dostál appears to be based on a rejection of the earlier combination subgenus *Microlophus* (DC.) Hayek. The rejection of Hayek's name appears to be due to Hayek's use of De Candolle's illegitimate sectional name (section *Microlophus* (Cass.) DC.) (see Article 33.4 in the International Code of Botanical Nomenclature; also see discussion above referring to De Candolle's series and sectional treatment). Dostál's combination should be rejected as a later homonym (Article 64.1 of the Code), whether or not one regards De Candolle's sectional names to have been invalidly published. Contemporary authors (Dostál, 1976; Wagenitz, 1955, 1975, 1980) have tacitly, if not explicitly, rejected De Candolle's series nomenclature by their acceptance of his sectional nomenclature.

genera to those that he considered most specialized. Jeffrey's list begins with *Warionia* Benth. & Coss., a genus assigned to the Mutisieae by Dittrich. The next nine taxa listed by Jeffrey were placed by Dittrich (1977) in the tribe Carlineae, and these were followed by *Echinops* and *Acantholepis* Less., of the tribe Echinopseae. The remaining taxa of Jeffrey's list were assigned to the tribe Cardueae by Dittrich, but Jeffrey's list intermixed taxa placed in the subtribes Centaureinae and Carduinae by Dittrich (1977). Jeffrey did not intend to indicate acceptance of taxa at the generic level by their inclusion in his list, except for the 11 genera (*Centaurea, Cirsium, Cnicus, Cyanus, Cynara, Echinops, Goniocaulon, Plectocephalus, Rhaponticum, Silybum, Volutaria*) included in his key to genera of East Tropical Africa. Jeffrey included *Cnicus, Goniocaulon, Plectocephalus,* and *Rhaponticum* in his key, even though they had not been recorded for this area. A more extensive key was presented by Jeffrey for 17 genera that he considered worthy of recognition apart from *Centaurea* on the basis of differences in filament and style-branch pubescence, characters Jeffrey found to correlate well with the pollen types established by Wagenitz (1955). He further noted that subgenus CENTAUREA is a small group more distinct from other members of *Centaurea sensu lato* than many groups that have been segregated as genera by earlier workers. For a consistent treatment, Jeffrey held that *Centaurea* would have to be restricted to subg. CENTAUREA. If such a system were adopted, however, Jeffrey believed that the numerous nomenclatural recombinations that would have to be made would result in a "clearly undesirable" situation. Jeffrey recognized nine subgenera of *Centaurea* based on filament and achene pubescence and the pollen types of Wagenitz.

The eight species of *Centaurea* (*C. americana, C. Calcitrapa, C. Cyanus, C. dubia, C. Jacea, C. maculosa, C. nigra, C. solstitialis*) found in the Southeast have, as noticed above, been placed in different subgeneric categories and, in some cases, different genera by European workers. *Centaurea americana* is the type species of *Plectocephalus* D. Don (Dostál, 1973), but within *Centaurea* it has been placed in sect. *Plectocephalus* (D. Don) DC. (Wagenitz, 1955; Dittrich, 1968a). Dostál (1976) incorrectly synonymized *C. dubia* under the later name *C. transalpina* Schleicher ex DC., a species that he included in subgenus *Jacea* sect. *Nigrescentes* (Hayek) Dostál. Hayek (1901), however, treated *C. transalpina* as a synonym of *C. dubia* in (subgenus *Jacea*) sect. *Eujacea* Hayek.

Centaurea Jacea, the type species of *Jacea* Miller (Dostál, 1973), and *C. nigra* were both placed in sect. *Jacea* (Miller) DC. (Wagenitz 1955, 1975; Dittrich, 1968a) and in subg. *Jacea* (Miller) Hayek (Clapham *et al.*). Dostál (1976) retained *C. Jacea* in subg. *Jacea,* sect. *Jacea,* but placed *C. nigra* in sect. *Lepteranthus* (DC.) Dumort. Since these two species frequently hybridize (see below), certain workers (Briquet, 1931; Wiegand & Eames) have considered them to be conspecific.

Centaurea Cyanus ($2n = 24$; Löve & Löve, 1961, as *Cyanus arvensis* Moench), the type species of *Cyanus* Miller (Dostál, 1973), was placed in subgen. *Odontolophus* (Cass.) Hayek by Dostál (1976) and in sect. *Cyanus* (Miller) DC. by Wagenitz (1975).

Centaurea maculosa ($2n = 18, 36$; Löve & Löve, 1961, as *Acrolophus maculosus* (Lam.) Cass.) has been placed variously in the genus *Acosta* Adanson

(Holub, 1972b), subg. *Acrolophus* sect. *Maculosae* (Hayek) Dostál (Dostál, 1976), and sect. *Acrolophus* (Cass.) DC. (Wagenitz, 1955; Hayek, 1901), while *C. Calcitrapa* ($2n = 20$; Löve & Löve, 1961, as *Calcitrapa stellata* Lam.), the type species of *Calcitrapa* Heister ex Fabr. (Dostál, 1973), has been placed in sect. *Calcitrapa* (Wagenitz, 1955, 1975) and subg. *Calcitrapa* (Dostál, 1976).

Centaurea solstitialis ($2n = 16$) has been placed in the genus *Leucantha* S. F. Gray (Löve & Löve, 1961), subg. *Solstitiaria* (Hill) Dobrocz. (Dostál, 1976; Clapham *et al.*), and sect. *Mesocentron* (Cass.) DC. (Wagenitz, 1955).

The only comprehensive treatment of *Centaurea* for the United States and adjacent Canada is that by Moore (1972), who treated 28 species. Within his key to species, taxa were grouped according to sectional characteristics. Moore & Frankton (1954) put forth cytological and morphological justification for segregating *C. repens* L., a widespread weed of the Western States, as *Acroptilon repens* (L.) DC. (see also Dostál, 1973).

Sectional classification based on pollen data (Wagenitz, 1955) was considered to be congruent with classifications based on involucral characters and chromosome number by Guinochet, who tentatively proposed that groups with high base chromosome numbers, nearly entire involucral bracts, relatively complex pollen structure (*Serratula* type), generally large capitula, large, entire leaves, and perennial habit gave rise to groups with lower chromosome numbers, complex involucral bracts, relatively simple pollen structure (*Jacea* type), normally small capitula, often deeply divided leaves, and annual or biennial habit.

Guinochet postulated base chromosome numbers of 8, 9, 10, 11, 12, 13, and 15 for *Centaurea.* His study of the karyotypes showed a correspondence between the size and the number of chromosomes. Guinochet hypothesized that the lower chromosome base numbers evolved from the higher ones by way of translocations and loss of chromosomes. These chromosomal mutations were considered by him to have played a primary role in the differentiation of species, subspecies, and varieties, and further that polyploidy had affected speciation in only a secondary manner.

Hypotheses of hybridization and introgression have been used to explain plants morphologically intermediate between taxa otherwise considered distinct (Arènes, 1948, 1949, 1957; Chiapella; Georgiadis; Marsden-Jones & Turrill; Roy). Other studies (Ockendon *et al.*; Elkington & Middlefell) have found little or no evidence of hybridization and claim that certain *Centaurea* species (e.g., *C. nigra* L.) are highly variable. In particular, the taxa included in sect. Jacea (including *C. Jacea, C. nigra, C. dubia,* and *C. nigrescens* of the Southeastern species) have been studied extensively, and the number of species recognized in this group has fluctuated from one (Briquet, 1902, 1931) or a few variable species (Guinochet) to as many as seven distinct ones (Arènes, 1957; Marsden-Jones & Turrill). All the species of this section have chromosome numbers of $2n = 22$ or $2n = 44$ (Guinochet; Guinochet & Foissac; Roy; Löve & Löve, 1961; Gervais; Moore, 1968; Marsden-Jones & Turrill).

Extensive and well-documented crossing experiments (Marsden-Jones & Turrill) indicate that *C. nigra* and *C. Jacea* produce fertile offspring when selfed and will, in general, breed true for characters of the involucre and flower color.

Hybrids between *C. Jacea* and *C. nigra* were readily evident, and backcrossing between hybrid offspring and the parental lines produced a wide range of flower and involucral characteristics. In some cases, interspecific crossing seemed to lead to abnormalities in the formation of the androecium. Marsden-Jones & Turrill reported that in some extensive hybrid swarms, pure forms of *C. Jacea* have disappeared.

The distribution of sesquiterpene lactones has been used in attempts to clarify taxonomic boundaries within both *Centaurea* and the subtribe Centaureinae (Geppert *et al.*; Nowak *et al.*; see above under tribal discussion), but no classification based on phytochemistry has been proposed to date. The numerous sesquiterpene lactones known from *Centaurea* have been reviewed by several authors (Wagner, Seaman, Nowak *et al.*, Geppert *et al.*) and will not be reiterated here.

Compounds isolated from species known from the Southeast include cynaropicrin from *C. americana* (Ohno *et al.*), cnicin from *C. Calcitrapa* (Jakupovic *et al.*), scabiolide from *C. Calcitrapa* and *C. solstitialis,* and chlorohyssopifolin A from *C. nigra* and *C. solstitialis.* (See Seaman for citations and sesquiterpenes known from *Centaurea* up to 1982.)

A wide variety of flavonoids, including three flavones (centaurein, jacein, jaceoside) from *C. Jacea* and two (swertisin, isoswertisin) from *C. Cyanus* (see Wagner for citations and structural components), has been reported from *Centaurea.*

Stevens (1982) and Stevens & Merrill reviewed the wide range of biological activity (cytotoxicity, phytotoxicity, actinioplasticity, and allergenicity, among others) attributed to sesquiterpene lactones and suggested that these compounds may play a role in the allelopathy attributed to *C. repens* and *C. solstitialis.* They concluded that these compounds affect root growth in a similar, yet more pronounced, manner to auxins, but do not affect seed germination.

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7. **Cnicus** Linnaeus, Sp. Pl. **2**: 826. 1753; Gen. Pl. ed. 5. 358. 1754, nom. cons.

Erect annual herbs, the stems branching, arachnoid-villous. Leaves of the lower stem commonly short-petiolate, upper leaves sessile; blades lanceolate, up to 20 cm × 5 cm, subcoriaceous, sinuate-dentate or pinnatifid, scarcely or

not at all decurrent, lower surface conspicuously veined and densely glandular, margins weakly spiny or ciliate. Capitula heterogamous, discoid, solitary at the end of branches, closely subtended by ovate or lanceolate cauline leaves. Involucre campanulate to ovoid, often obscured by cauline leaves; bracts imbricate, multiseriate, ovate-lanceolate, the outer mucronate-subulate, the inner longer, with a pectinate to spine-like apical appendage. Receptacle flat; scales numerous, setaceous. Outer flowers inconspicuous, sterile, with a very slender 2- or 3-lobed corolla; inner flowers perfect, their corollas slightly zygomorphic, yellow, glabrous or minutely glandular, with the tube narrow, elongate, ca. 8–10 mm long, the throat expanded, slightly saccate, unequally divided by the sinuses of the lanceolate, glabrous corolla lobes with two sinuses considerably deeper than the other three. Staminal filaments pubescent, connected at base of throat; anthers stramineous with a firm, narrow, apical appendage, shortly saggitate tailed at base. Style smooth below a distinct collar of hairs at base of the short, scarcely divergent, papillate branches. Achenes obliquely attached to receptacle, ca. 8 mm long, subterete, strongly 20 ribbed, glabrous, with a firm 10-toothed crown. Pappus biseriate, the outer of 10 long, minutely scabrid, stramineous awns, alternating with 10, much shorter, white, minutely hairy and sparsely pectinate inner bristles. (*Carbenia* Adanson.) TYPE SPECIES: *C. benedictus* L., typ. cons. (See Hitchcock & Green, Nomencl. Prop. Brit. Bot. 179. 1929, for discussion.) (A Latin name of the safflower (*Carthamus* L.), from Greek *cnecos*.)—BLESSED THISTLE.

A single species of the Mediterranean region widely naturalized in many parts of the Northern Hemisphere.

Cronquist (1980) characterized *Cnicus benedictus* in the Southeast as sparingly established in fields and waste places. This species is found scattered throughout the Piedmont and along the Coastal Plain from Virginia, south through Georgia and Alabama, but apparently it neither extends as far west as Texas (Correll & Johnston), nor is it found in the Great Plains flora (Barkley, 1986).

Linnaeus included five species in his treatment of *Cnicus*. Adanson recognized the genus *Carbenia* for two species, one of which was *C. benedictus*. Apparently unaware of Adanson's *Carbenia*, Gaertner redefined *Cnicus* as a monotypic genus based on the unique pappus characters of *C. benedictus*. Persoon incorporated *Cnicus* as a subgenus of *Carduus*, but treated *Cnicus benedictus* as a member of *Centaurea* subgenus *Calcitrapa*. While Don recognized *Cirsium* and placed therein many taxa treated by earlier authors under *Cnicus*, he, too, treated *C. benedictus* under *Centaurea* (sect. *Calcitrapa*). Lessing's recognition of *Cnicus* for *C. benedictus* was followed by De Candolle, who provided an extensive list of excluded species. Both Lessing and De Candolle placed *Cnicus* in the subtribe Centaureinae. Bentham recognized *Carbenia* Adans. for *Cnicus benedictus* and broadly circumscribed *Cnicus* to include many taxa currently placed in *Cirsium*. Neither Hoffmann nor Spach followed Bentham but treated *Cnicus* as it was delineated by Gaertner. Asa Gray (1884a, b, 1874), on the other hand, did follow Bentham's circumscription (see discussion under *Cirsium*) and included *Cnicus benedictus* in *Centaurea*. Such

nomenclatural confusion led to the conservation of *Cnicus* L. emend. Gaertner in 1935 (Hitchcock & Green). Contrary to most floristic treatments of the past fifty years, Ahles in Radford *et al.* placed *Cnicus* in synonymy under *Centaurea* from which it is readily distinguished by its pappus structure and fruit characters (Dittrich, 1970).

Chromosome numbers reported for *Cnicus benedictus* are $2n = 20$ and $2n = 17$ (see Mehra *et al.*; Goldblatt, 1981, for references).

Medicinal qualities have been attributed to *Cnicus* (Franco) particularly for the glucoside cnicin for its antimicrobial and antibiotic activity (Wagner; Schneider & Lachner; Vanhaelen-Fastré) and for treatment for gout (Mabberley). In addition to cnicin, another sesquiterpene lactone, salonitenolide, and monoterpenes have been isolated from *C. benedictus* (Seaman).

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Under tribal references see Adanson; Barkley, 1986; Bentham, 1873a; Bobrov & Czerepanov; De Candolle; Correll & Johnston; Cronquist, 1980; Don; Gaertner; Goldblatt, 1981; Gray, 1874, 1884a, b; Hegi, 1928–29, 1987; Hoffmann; Lessing; Mehra *et al.*; Morton; Munz; Persoon; Radford *et al.*; Seaman; Spach; and Wagner.

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THE GENERA OF MELIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

NORTON G. MILLER[2]

MELIACEAE A. L. de Jussieu, Gen. 263. 1789, 'Meliae', nom. cons.

(MAHOGANY FAMILY)

Small to large trees [shrubs, or rarely suffrutescent herbs]; new growth from terminal buds or from axillary buds, if axillary, then the branch apices dying back at end of growing season; bud scales imbricate [or absent], pubescent or not, deciduous; pith homogeneous [or with clusters of fibers]; new growth near leaf insertions with or without extrafloral nectaries. Leaves alternate, exstipulate, once or twice odd- or even-pinnate [trifoliolate, or simple]; spirally arranged [rarely decussate]; trichomes of young leaves simple and hooked, glan-

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible through the support of National Science Foundation Grant BSR-8716834 (N. G. Miller, principal investigator), under which this account was largely prepared, and BSR-8717333 (C. E. Wood, Jr., principal investigator). The 135th in the series, this paper follows the format established in the first one (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ]. The references that I have not verified are marked with asterisks.

Several botanical colleagues helped in various ways in the preparation of this paper, particularly C. E. Wood, Jr., W. J. Crins, G. C. Tucker, I. A. Al-Shehbaz, G. K. Rogers, T. J. Rosatti, B. G. Schubert, and B. T. Styles, all of whom provided information, perspectives on the taxonomic literature, and/or comments on a draft of the manuscript. I also thank Stephen A. Spongberg for his editorial review of the manuscript. The staff of the New York State Library, and especially Alta Beach, Senior Librarian, and of the Libraries of the Arnold Arboretum and Gray Herbarium, Harvard University, gave prompt assistance with the sometimes challenging task of satisfying my pleas for literature that was hard to acquire. Specimens housed in the combined herbaria of the Arnold Arboretum and Gray Herbarium and the herbarium of the New York State Museum, as well as liquid-preserved materials gathered in Florida by Carroll Wood and collaborators, and a plant of *Swietenia Mahagoni* under cultivation in the Harvard University Herbaria Building were used in this study. Cheryl Tribley, Shirley Rabideau, and Barbara Nimblett efficiently prepared the typescript.

The illustration of *Melia Azedarach* was drawn by Arnold D. Clapman under the supervision of G. K. Brizicky and C. E. Wood, Jr. In FIGURE 1 all drawings are of liquid-preserved specimens; a is from material collected by Wood and A. Strahler at Fort Meade, Florida; b and c are from plants collected north of Brooksville, Florida, by Wood, K. A. Wilson, and G. R. Cooley; and d–g are based on plants collected at Salem, Virginia, by Wood. In FIGURE 2 all drawings are based on fresh (h–n) or liquid-preserved (a–g) material collected by D. Sturrock in West Palm Beach, Florida; a–g and n are by Rachel Wheeler (with dissections by Wood), h–m are by Sue Sargent.

This paper is published as Contribution Number 654 of the New York State Science Service.

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Journal of the Arnold Arboretum **71:** 453–486. October, 1990.

dular, dendritic, or stellate [or peltate scales]; leaflets symmetrical or asymmetrical, serrate or entire, deciduous with rachis or not [rachis rarely winged, sometimes with an intermittently growing terminal "bud"]. Plants polygamous or monoecious [or rarely dioecious]; inflorescences axillary, large or small bracteate thyrses [panicles, or rarely spikes, sometimes cauliflorous or ramiflorous, or flowers epiphyllous], cymules 3-flowered, the terminal (first-opening) flower perfect or carpellate, lateral flowers staminate; staminate flowers deciduous after anthesis. Flowers regular (actinomorphic); in *Melia* perfect and staminate flowers similar at anthesis, in *Swietenia* staminate and carpellate flowers dimorphic. Sepals [2–4 or]5(6)[or 7], separate or fused basally and calyx then 5-(rarely 4- or 6-)lobed [or calyx circumscissile]. Petals [3, 4]5(rarely 6)[8 or 14], free [or sometimes fused below to staminal tube], in 1 [or rarely 2] whorls, glabrous or pubescent abaxially, alternate with the sepals, the aestivation convolute, imbricate [or contorted or valvate]. Stamens united into a cylindrical or urn-shaped [cyathiform] tube [or filaments free], tube fringed [or not] with [8 or 9]10(or 12) teeth, individual teeth deeply cleft or not; anthers [3–]10(12)[–23], [rarely septate], in one [rarely 2] whorl[s], sessile on inside [or top] of tube [or with short filaments from top of tube], basifixed or dorsifixed, glabrous [or pubescent], alternating with the teeth or seemingly opposite two narrow teeth, dehiscence introrse, connective short [or sometimes greatly prolonged and filiform]; pollen [3- or] 4-colporate. Gynoecium syncarpous, the ovary superior [very rarely inferior], [3–](4)5 or 6[–15]-locular, each locule with 2 superposed ovules or with numerous ovules in 2 rows [ovules sometimes few and collateral], the placentation axile [rarely parietal], ovules anatropous, nectariferous disc annular, entirely below the ovary or extending slightly upward, obscurely lobed and free from the ovary [or cyathiform, tubular, rarely a stipe supporting the gynoecium, or absent]. Ovary in perfect flowers pyriform and tapered into a long style, stigma rounded, scarcely wider than style; in carpellate flowers ovary globose, style short, stigma discoidal and nearly as wide as mouth of staminal tube [or obconical, globose-capitate, or 3–6-lobed], anthers withered [staminodia rarely present]; in staminate flowers ovary narrowly pyriform, style abruptly differentiated and longer than in carpellate flowers, stigma discoidal. Fruit a drupe, endocarp 5- or 6-locular, keeled, usually one seed per locule [or endocarps separate, thin or thick walled] or a 5-locular capsule, septicidally [loculicidally] dehiscent from base [or apex], columella persistent, [or fruit a fleshy or leathery berry, or very rarely a nut]. Seeds retained within the endocarp or winged and dispersed after capsule dehiscence [commonly with a brightly colored arillode or sarcotesta]; cotyledons collateral, longer than broad or broader than long, embryo short, straight [or curved], plumules minute or absent; endosperm fleshy, oily or more commonly thin and appearing absent; germination phanerocotylar or cryptocotylar. (Including Cedrelaceae R. Brown in Flinders, Voy. Terr. Austral. **2:** 595, 1814, "Cedreleae"; tribe Aitonieae Harvey in Harvey & Sonder, Fl. Capensis **1:** 243. 1860 [Sapindaceae].) TYPE GENUS: *Melia* L.

A mainly tropical family of moderate size (50 genera, 550 species, according to recent monographic study; Pennington & Styles), with 14 genera (eight native,

six introduced) represented in the New World. Only *Cabralea* A. Juss. (one sp.), *Ruagea* Karsten (ca. five spp.), *Cedrela* P. Browne (seven spp.), *Schmardaea* Karsten (one sp.), and *Swietenia* Jacq. (three spp., one in our area) are endemic to the Western Hemisphere; *Trichilia* P. Browne (85 spp.; largely lowland tropical America, some species in Africa and a few in the Indo-Malayan region), *Guarea* Allamand ex L. (35 spp. in tropical America, five in tropical Africa), and *Carapa* Aublet (two spp.; tropical America and Africa) are disjunctly distributed among portions of the New and Old World tropics. Of the introduced genera only one species of *Melia* L., *M. Azedarach* L., is widely established in tropical and warm temperate parts of North and South America, including the southeastern United States.

Over the past 20 years a great deal of new and important information has been discovered about the taxonomy of the Meliaceae, mainly by botanists associated with the Commonwealth Forestry Institute, University of Oxford, England. Their studies have been wide ranging; those pertaining to generic concepts are summarized by Pennington & Styles in a lengthy paper that contains many original observations and new analyses and interpretations. In addition the family has been monographed for the *Flora Neotropica* series (Pennington, 1981), and many problems involving difficult species complexes have been clarified, in part aided by the recent availability of new and more adequate collections and a better understanding of the biology—especially the floral biology—of the family.

The Meliaceae, excluding the Ptaeroxylaceae J. F. Leroy, are a reasonably coherent group of monoecious, dioecious, or polygamous woody plants (generally trees), mostly with alternate, pinnate leaves and regular pentamerous flowers containing a staminal tube and a hypogynous nectariferous disc. Four subfamilies are recognized (Pennington & Styles), two of which are represented in our area. Subfamily Melioideae [Harms] (plants polygamous or dioecious, ovules 1 or 2, superposed or collateral, fruit a drupe, berry, or loculicidal capsule, seeds not winged, rays of wood usually 1 or 2 seriate) contains *Melia Azedarach,* a naturalized tree in our area, in tribe Melieae [DC.]. Six additional tribes accommodate genera represented in the neotropics, paleotropics, or both. Subfamily Swietenioideae Harms (plants monoecious, ovules usually many in two rows, fruit a septicidal capsule with a central columella, seeds winged, rarely otherwise, rays of wood generally 3–6 cells wide) includes *Swietenia* and eight other genera in tribe Swietenieae (A. Juss.) Spach,[3] plus two additional tribes that include neotropical and/or paleotropical genera not represented in our area. In general the flowers of members of the Swietenioideae are small or

[3]Adrien de Jussieu in his "Mémoire sur le Groupe des Méliacées" recognized two families, Meliaceae and Cedrelaceae, which he divided into groups of genera, providing a name for each group and Latin diagnoses but no designation of rank. Spach (Hist. Nat. Vég. Phan. **3**: 161–205. 1834) used the rank tribe for De Jussieu's groups. The De Jussieu "Mémoire" was published in 1832 (1830 is the year on the title page of volume 19 of Mém. Mus. Hist. Nat. Paris in which the monograph was published, but the volume was issued in 1832; see Pennington, 1981, p. 4). The names and diagnoses of the new species and the subfamilial groups proposed by De Jussieu were, however, published in 1830 (Bull. Univ. Sci. Industr. Sect. 2 (Bull. Sci. Nat. Géol.) **23**: 234–241) and also prior to 1832 in Linnaea **6**(Lit.): 107–115. 1831.

sometimes minute, in contrast to the larger, more showy flowers of members of the Melioideae.

Two monotypic subfamilies, Quivisianthoideae Pennington & Styles and Capuronianthoideae Pennington & Styles, accommodate genera endemic to the Malagasy Republic. The poorly known *Quivisianthus* Baillon in Grandidier has flowers similar to certain members of the Melioideae but differs substantially from them and other genera in the subfamily in having a loculicidal capsule and dry winged seeds. *Capuronianthus* J. F. Leroy is like members of the Swietenioideae in having a septicidal capsule, but it has naked buds, decussate leaves, and two superposed ovules (with two others aborting). Thus these subfamilies have certain characteristics of either the Melioideae or Swietenioideae, as well as some unique features.

Much is known about the chromosome cytology of the Meliaceae. About 100 species (of the ca. 550 species in the family) have been studied (Styles & Khosla), and this work has revealed greater variation in chromosome numbers ($2n$ = 12 to ca. 360) than has been found in other woody, mainly tropical angiosperm families. Most counts are of mitotic figures from root tips (Styles & Khosla), although some counts are based on anther squashes. In many species the chromosomes are minute (0.5 to 3.5 μm), even in cells of the root tip. Accurate determination of the higher numbers has been difficult because of staining problems (Datta & Samanta) and chromosome size. Most chromosomes have submedian to median centromeres. Polyploid series are present in some genera (e.g., *Chisocheton* Blume and *Dysoxylum* Blume of the Indo-Malayan region south to Australia and/or New Zealand). Within species variation in chromosome number (polyploidy, aneuploidy) is also known, for example, in *Swietenia, Toona* (Endl.) M. J. Roemer, and other genera. There is considerable disagreement about chromosome base numbers in the Meliaceae. Some authors have suggested $x = 7$ (Mehra *et al.*). Others cite evidence favoring two base numbers, $x = 6$, $x = 7$ (Khosla & Styles) or multiple base numbers, $x = 9, 10, 11, 12, 13, 14$ (Datta & Samanta). The most frequent haploid chromosome number in the family is 25. Chromosome numbers and karyotypes do not generally provide independent substantiation for subfamilies and tribes defined on the basis of morphology.

Flower morphology is extremely diversified in the Meliaceae. Characteristics of the androecium are particularly useful taxonomically at the generic level. The filaments are generally connate into a staminal tube (the shape of which may differ considerably among genera) or rarely are free. The anthers are inserted in the throat of the tube or at its summit, and they either are sessile or have short extensions of the filaments. Teeth occur along the distal edge of the tube, and the shape of these differs in taxonomically significant ways. The shape of the nectariferous disc, which is always located below the gynoecium, is also variable, as is the shape of the stigma. The patterns these structures present may be consistent within or among genera.

It has been suggested that the variability in floral structure may reflect adaptations for specific insect pollinators (White, in Pennington & Styles). However, the pollination biology of the family has been incompletely investigated. The flowers of some species are reported to be fragrant. This suggests insect

pollination, as does the uniform presence of floral nectaries. Flowers of *Guarea rhopalocarpa* Radlk. open at night and are probably moth pollinated (Bullock *et al.*). Moths were found to pollinate various species of *Guarea* and *Cedrela* in Costa Rica (Bawa *et al.*, 1985), and hymenoptera have been seen to effect pollen transfer in *Trichilia havanensis* Jacq. (White, in Pennington & Styles).

It has only recently been realized that genera characterized by perfect flowers are unusual in the Meliaceae (Lee, 1967; Styles, who mentioned that this condition was restricted to *Turraea* L. and a few related genera; suspected also in some species of *Guarea* (Pennington, 1981)). What numerous authors in the past have described as perfect flowers are in reality either functionally staminate or functionally carpellate. In some cases (e.g., *Swietenia*) the carpellate and staminate flowers are conspicuously dimorphic, in others (e.g., *Melia*) the staminate and perfect flowers are superficially similar but can be told apart by inspection of the ovules, which appear aborted even in young staminate flowers. Poor staining quality of pollen or withered anther sacs characterize the functionally carpellate flowers, which only rarely have obvious staminodia.

It may be necessary to study plants in the field to ascertain whether a species is monoecious, dioecious, or polygamous. The reason for this, as Pennington (1981) points out, is that the staminate flowers are deciduous soon after anthesis, and they may not be present in herbarium specimens. In some dioecious species (e.g., *Trichilia Poeppigii* C. DC., of northwestern South America) not only are the flowers dimorphic, but the inflorescences are as well. A Costa Rican population of the dioecious *Guarea rhopalocarpa,* carefully followed for two years (Bullock *et al.*), showed complex patterns of flowering and fruiting in discrete episodes at irregular intervals during the study period, with two or three episodes per year per tree. Flowering occurred discontinuously over nine months of the year, and certain individuals flowered more or less at the same time. Trees with staminate or carpellate flowers were in about even proportion, but the number of staminate inflorescences during the census period was nearly always much greater.

Mechanisms of fruit and seed dispersal are also varied in the family. In many members of subfam. Melioideae the outer integument of the ovule becomes elaborated into a small or large sarcotesta, which can be rich in oils. The details of development of this structure are poorly known in most genera, but in some species it appears to originate from a specific part of the ovule. The meliaceous sarcotesta does not seem to be a proliferation of the funiculus, and therefore it is not exactly equivalent to an aril. In species with dehiscent fruits the sarcotesta is red or orange, and it contrasts with the black or brown unmodified seed coat. Such bright colors attract bird or mammal disperal agents.

Seed disperal in *Guarea glabra* Vahl, an understory tree producing abundant fruit, has been studied in Panama (Howe & De Steven). Seventy percent of the visits and 60 percent of the seeds removed involved four North American migrant birds (great crested flycatcher, Swainson's thrush, red-eyed vireo, and Tennessee warbler). Fruiting and the northward migration of these birds were synchronized. Of ten species of *Aglaia* Lour. studied by Pannell & Kozioł in Malaysia and Indonesia three had dehiscent fruits revealing seeds with a red sarcotesta (bird-dispersed), and seven had indehiscent fruits and seeds with a

yellow, white, or translucent sarcotesta (five of these were primate-dispersed). More lipids were present in sarcotestas associated with bird dispersal; the coverings of the primate-dispersed seeds were gelatinous, low in lipid content, and high in sugars.

Bats are likely to disperse the fleshy fruits (and endocarps) of *Azadirachta indica* A. Juss. in West Africa (Ayensu) and perhaps elsewhere in the tropics. Fruits of *Melia Azedarach* are eaten and dispersed by birds in the United States and by birds and fruit bats in South Africa (White, 1986). Seeds of *Carapa guianensis* Aublet are eaten by rodents, monkeys, and wild pigs, which may be agents of dispersal (White, 1983). The buoyant seeds of this species, which prefers swamp forests in at least part of its range, are transported by water (*ibid.*). In Amazonia several kinds of fish have been observed to eat the seeds of *C. guianensis,* but the seeds appear to be destroyed in the process (Gottsberger). Wind is the presumed dispersal agent for those species (mainly members of subfam. Swietenioideae) with dry, winged seeds.

Published morphological and anatomical studies of the Meliaceae have dealt mainly with wood anatomy and aspects of vegetative structure that are unusual in seed plants.

The early investigations of Kribs and of Panshin into the secondary xylem of representatives of the family yielded character sets that for many years were thought to be diagnostic for genera. However, wood of about one-half of the known species of Meliaceae has now been examined (Pennington & Styles), and some of the conclusions drawn by Kribs and Panshin are no longer tenable. Few genera of the Meliaceae can be distinguished on the basis of wood anatomy alone, but anatomical characters sometimes correlate with other morphological ones in taxonomically significant ways. Wood provides characters (e.g., fibers septate, terminal bands of apotracheal parenchyma absent vs. fibers nonseptate, apotracheal parenchyma present) that are helpful in delimiting subfamilies, and within the Melioideae in placing genera in tribes.

Leaves (as well as the bark and secondary xylem) of many Meliaceae have secretory cells. In leaves they are located in the mesophyll and with back lighting are visible as translucent dots. (Secretory cells are evidently lacking in *Melia Azedarach* and *Swietenia Mahagoni,* however.) The pinnate leaves of species of *Guarea* are unusual (Skutch) because they exhibit intermittent, indeterminate growth from a crozier-like "bud" at the rachis apex, which remains meristematic. On the basis of anatomy and development such "leaves" are leaf homologs, although in their continuous growth (including increases in secondary xylem thickness) they are analogous to branches (Steingraeber & Fisher). Experiments performed by Fisher showed that leaflets in *G. Guidonia* (L.) Sleumer exhibited either a "sun" or a "shade" morphology and that within a given leaf the expression of one form or the other was plastic and related to whether the leaflets were initiated in the shade or in the sun. Leaves of *G. rhopalocarpa* are estimated to be 7–11 years old at abscission (Skutch). Such indeterminate leaves are also found in species of *Chisocheton,* a few species of which also have few-flowered, epiphyllous inflorescences. Vascular bundles supplying such inflorescences arise from the stele of the rachis with no evidence that the bundles are adnate to the rachis vasculature (Mabberley, 1979).

Basal leaflets in some Meliaceae are modified into stipule-like structures that are appressed to the leafbase-stem junction. The point of attachment is, however, the leaf rachis. Pseudostipules of varying form occur in species of *Trichilia* (Pennington, 1981), and they are known also in some other families of the Rutales (e.g., Sapindaceae; Weberling & Leenhouts). Sac domatia occur on the abaxial surfaces of leaves of *Dysoxylum Fraseranum* Benth. of Australia (Metcalfe & Chalk, 1979).

The palynology of the Meliaceae has been summarized by Pennington & Styles on the basis of studies of about two-fifths of the species in the family, including representatives of all genera. The family is stenopalynous, with little variation from the basic pattern (pollen subprolate or prolate-spheroidal, 3- or 4-colporate, psilate, sometimes verrucose) among genera or even subfamilies. Pollen has been helpful in the placement of certain genera once included in the Meliaceae, for example *Flindersia* R. Brown in Flinders to the Rutaceae and *Ptaeroxylon* Ecklon & Zeyher (which has neither meliaceous or rutaceous pollen) to the Ptaeroxylaceae (with *Cedrelopsis* Baillon). *Turraea* and allied genera (pollen generally oblate-spheroidal, 3-colporate, exine scabrous to verrucose) are the most disparate elements in the family palynologically. Pollen is of limited value in defining genera.

Chemotaxonomic studies of the Meliaceae have focused largely on the distribution and systematic significance of limonoids, a group of oxidized triterpenes otherwise known to occur in the Rutaceae and Cneoraceae. These secondary metabolites impart a bitter taste to the plant tissues in which they occur. A mixture of limonoids is present in most species, and different limonoids may be present in different parts of a plant (Taylor, 1983). Sometimes limonoids occur in only one plant organ. Only the most highly oxidized limonoids appear to be significant taxonomically. Various kinds of limonoids are partitioned in mostly nonoverlapping patterns among the Meliaceae, Rutaceae, and Cneoraceae, and within the Meliaceae between subfamilies Melioideae and Swietenioideae, but less clearly among the tribes recognized by Pennington & Styles. *Melia* and *Azadirachta* A. Juss. (both in tribe Melieae) have many limonoids in common, although *Azadirachta* has some that are lacking in *Melia* (Taylor, 1983). Alkaloids are reported from only five members of the Meliaceae (Mester), and coumarins are known in relatively few genera (Gray). Flavonoid chemistry has not been much used as a chemotaxonomic tool in the family (Harborne), and it is unclear how much potential it has.

The paleobotanical record of the Meliaceae consists of pollen, leaves, seeds, and fruits, mainly of Tertiary age. A few Cretaceous fossils have been attributed to the family (e.g., Graham, 1962). Structurally preserved wood from the Tertiary of Europe and North Africa is similar to that of the extant genera *Carapa, Entandrophragma* C. DC., and *Lovoa* Harms (Louvet, 1973, 1975; Mädel; Selmeir, 1983, 1987), and these occurrences are cited as examples of tropical or subtropical elements in pre-Quaternary paleofloras of the Mediterranean Basin region. *Cedrela* is represented by leaves, fruits, and pollen in the Eocene and Miocene floras of the western United States (MacGinitie; MacGinitie *et al.*). Dispersed pollen of *Cedrela* and/or *Guarea* has been recovered from Oligocene and Miocene sediments in the Caribbean Basin (Graham & Jarzen;

Graham, 1977). These occurrences suggest possible migrational tracks and temporal limits for the migration of neotropical plant elements occurring in the Tertiary paleofloras of the southeastern United States. The absence of palynological diversification and distinctive pollen types in the Meliaceae may limit how much information can be obtained from studies of dispersed fossil pollen.

Most members of the Meliaceae are forest trees, usually reaching the canopy or subcanopy, but sometimes only the understory. In the Neotropics the family is especially well represented in nonflooded lowland rain forest (terra firma) and in seasonally flooded lowland forest (várzea). Various genera are also represented in montane forests and sometimes in the cloud forests of central and northern South America. Certain species grow on drier sites, especially in the West Indies where species of *Trichilia, Guarea,* and *Cedrela* occur on dry (sometimes mesic) soils over limestone hills. *Xylocarpus granatum* Koenig and *X. mekongensis* Pierre, are mangroves, occurring in parts of the area from East Africa to tropical Australia and Polynesia (Tomlinson).

The family is of considerable commercial importance, primarily as a source of valuable timbers that are used to make high quality furniture. *Khaya* A. Juss., African mahogany, species of *Swietenia,* the true mahoganies, and species of *Entandrophragma* of tropical Africa yield perhaps the most valuable hardwood lumbers. A limonoid, azadirachtin, extracted from the seeds of *Azadirachta indica* A. Juss., neem tree, has elicited much interest as a growth inhibitor and an antifeeding agent against insects. Azadirachtin is presently under study for possible use in the control of insects that cause damage to food and other crop plants (Schmutterer & Ascher). Oil is extracted from seeds of species in a number of genera (Vaughan). Fruits of *Lansium parasiticum* (Osbeck) Sahni & Bennet (*L. domesticum* Jack), langsat, and *Sandoricum Koetjape* (Burm. f.) Merrill, santol, are eaten in Southeast Asia. The former is considered to be one of the best fruits of the Malayan region (Popenoe).

The Meliaceae are placed in the Rutales (Dahlgren *et al.,* Takhtajan, Thorne) or Sapindales (Cronquist), both of which are variously circumscribed. There is general agreement, however, that these orders are allied and form a distinct evolutionary line, linked directly to magnolioid ancestors (Meeuse). Phytochemical markers (triterpenes), in addition to morphological criteria, indicate close evolutionary relationships among the Meliaceae, Simaroubaceae, and Rutaceae. Limonoids are known from the Meliaceae and Rutaceae, whereas quassinoids, which are biochemically derived from them, are restricted to the Simaroubaceae (Seigler), suggesting that the Simaroubaceae are advanced, at least in this character.

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Key to the Genera of Meliaceae in the Southeastern United States

General characteristics: *Small to large trees; leaves alternate, exstipulate, once or twice odd-pinnate or even-pinnate; plants monoecious or polygamous; inflorescences axillary thyrses; flowers perfect, staminate, or carpellate (if only staminate and carpellate, then dimorphic), regular, pentamerous; sepals free or fused basally; petals free; stamens hypogynous, united into a fringed tube, or tube ending in deltoid teeth, anthers sessile; gynoecium syncarpous, 5-locular, stigma rounded, as wide as the style, or stigma discoidal, wider than style; ovules two, superposed, or many in 2 rows; fruit a drupe or a septicidal capsule splitting from base to apex; seeds remaining in endocarp or seeds free and winged.*

A. Leaves once to twice odd-pinnate, leaflets serrate; flowers large, showy, perfect and staminate flowers isomorphic; sepals separate; staminal tube fringed with narrow teeth; stigma rounded, as wide as the elongate style; nectariferous disc inconspicuous; fruit a drupe ..... 1. *Melia.*

A. Leaves even-pinnate, leaflets entire; flowers small, whitish, staminate and carpellate flowers dimorphic; sepals fused basally, staminal tube terminating in a ring of deltoid teeth; stigma discoidal, style narrow, short or long, nectariferous disc conspicuous, orange; fruit a septicidal capsule ..... 2. *Swietenia.*

Subfam. MELIOIDEAE [Harms in Engler & Prantl, Nat. Pflanzenfam. III. **4:** 267. 1896.]

1. **Melia** Linnaeus, Sp. Pl. **1:** 384. 1753; Gen. Pl. ed. 5. 182. 1754.

Small [to large] trees [or shrubs]; branch apices dying back, new growth initiated from axillary buds; bud scales stellate pubescent. Leaves deciduous, once to twice, rarely thrice, odd-pinnate, a pair of glands (extrafloral nectaries?) located on new branches near leaf insertions; young leaves with a mixture of dendritic (or stellate) hairs and simple, hooked hairs; leaflets petiolulate, mostly symmetrical at base, acuminate, serrate. Plants polygamous; inflorescences borne in the axils of the early leaves, terminal flower of cymule perfect, lateral flowers staminate; perfect and staminate flowers similar at anthesis. Sepals 5(6?), mostly free. Petals 5(6?), weakly [or strongly] pubescent abaxially, alternate with the sepals. Staminal tube cylindrical, outer surface smooth or with linear appendages, inner surface with long hairs, tube 20(24?)-toothed; anthers 10(12?), sessile, basifixed, inserted inside the tube opposite pairs of teeth, as long as the teeth and bent inward over the stigma at anthesis, connective slightly prolonged; pollen ± prolate, exine smooth to slightly scabrate. Ovary 5- or 6-locular, each locule with 2 superposed, anatropous ovules, style long-cylindrical, ending in a hemispherical stigma (style head) with five or six inwardly bent lobes [or lobes erect]; nectariferous disc annular, obscure, entirely below the ovary. Fruit a ± globose [or ovoid] drupe, endocarp spheroidal [or narrowly ellipsoidal], keeled, 5- or 6-locular, or locules fewer by abortion; one, rarely

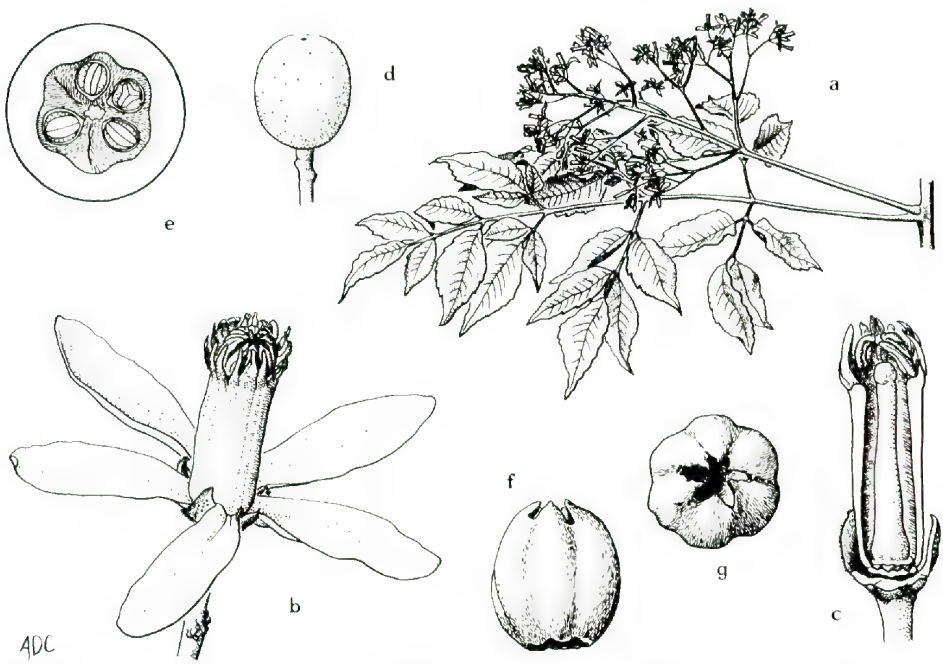

FIGURE 1. **Melia.** a–g, *M. Azedarach:* a, inflorescence and leaf, × ¼; b, flower, × 3; c, staminate flower in partial vertical section (petals and two sepals removed), showing gynoecium, nectariferous disc, staminal tube, appendages, and anthers, × 4; d, fruit (drupe), showing scars of staminate flowers on pedicel, × 1; e, fruit in diagrammatic cross section, showing 6-locular stone, 2 locules without seeds, endosperm stippled, embryos with 2 or 3 cotyledons, × 2; f, stone, from side, × 2; g, stone, from above, × 2.

two seeds per locule. Seed coats thin, brown; embryo ellipsoid, cotyledons flat, longer than broad, plumule minute; endosperm conspicuous, fleshy, oily. LECTOTYPE SPECIES: *M. Azedarach* L.; see N. L. Britton, N. Am. Trees 593. 1908. (Ancient Greek name for manna ash [*Fraxinus Ornus* L.].)—CHINABERRY.

A small genus indigenous to temperate, subtropical, and tropical regions of Asia and Africa, with one species, *Melia Azedarach,* chinaberry, China tree, pride of India, Carolina mahogany, $2n = 28$, introduced into the Americas where it is now widely naturalized. The original range of *M. Azedarach* may be impossible to ascertain because the species occurs throughout a large part of warm-temperate and tropical Asia. Hiern (in Hooker) noted that *M. Azedarach* was "wild in the sub-Himalayan tract, alt. 2–3000 ft."; Rechinger reported that *M. Azedarach* was spontaneous in the western Himalayas. Other authors (e.g., Coode & Cullen) concluded that it is native to India and China. Mabberley has recently contended that its native range encompasses portions of the area from Nepal, India, Burma, and southern China, through parts of the Malay Archipelago to New Guinea, the Solomon Islands, and tropical Australia (see discussion that follows).

The introduction of *Melia Azedarach* into the United States is credited to André Michaux, who is said to have grown it in his garden near Charleston,

South Carolina, in the late eighteenth century. At the close of the second decade of the 1800's, F. A. Michaux reported that *M. Azedarach* had become abundant in coastal areas of the southern United States, and, about the same time, Elliott, in reference to South Carolina and Georgia, wrote that it was "perfectly naturalized" and "springing from seed in cultivated land and around enclosures." It is now widely grown and self-seeding throughout our area except in the mountains. Mabberley suggested that plants in North America seemed to have at least two distinct origins, viz. from Indian plants via the Middle East and from Chinese plants via Japan.

The cultivar 'Umbraculifera', Texas umbrella tree, $2n = 28$, with a dense, flattened crown of foliage and the main branches radiating from the trunk like the supports of an umbrella, was first observed in Texas (where it may have originated). Most of the naturalized trees are of a much more open form. The Texas umbrella tree is widely planted in the southeastern United States.

Propagation of *Melia Azedarach* for horticultural purposes is from seeds or cuttings. The seeds germinate while they are still enclosed in endocarps, and one fruit may produce up to four seedlings. Germination percentages are usually high. Precocious flowering (sometimes even in the seedling stage) has occasionally been observed (van Steenis).

The circumscription of *Melia* is uncertain. Most authors state that the genus consists of 15 or fewer species, but it may actually contain about five species (Pennington & Styles, family references), or probably even a smaller number. Jacobs emphasized several important differences between *Melia* and *Azadirachta* A. Juss., which are sometimes treated as congeneric. The latter consists of two species, *A. indica* A. Juss. (*M. Azadirachta* L.), neem, a tree cultivated throughout India and held sacred by the Hindus, and *A. excelsa* (Jack) Jacobs of the Indo-Malayan region. Some of the characters that distinguish *Melia* and *Azadirachta* are: leaves twice- or thrice-pinnate vs. once-pinnate; large extrafloral nectaries(?) near petiole bases, one pair (both circular) vs. two pairs (one pair circular, the other linear); ovary 4–8-locular vs. 3-locular; style broad, stigma 4–6-lobed vs. slender and 3-lobed; and ovules superposed vs. collateral. However, Corner (family references) questioned whether *Azadirachta, Melia,* and *Cipadessa* Blume have been distinguished satisfactorily. He also mentioned that seeds of species of *Melia* and *Cipadessa* are similar.

Flowers and fruits of *Melia Azedarach* have been illustrated and described repeatedly. Less well-known species of *Melia* are included in various standard floras and other works that treat tropical or subtropical Asia or Africa. While numerous names exist for the considerable morphological diversity presented by the Asian plants, Mabberley concluded that only one polymorphic species, *M. Azedarach,* exists in that region. He proposed an informal infraspecific classification for *M. Azedarach* that consists of three categories, wild plants (incl. *M. dubia* Cav., *M. composita* Willd., *M. australasica* A. Juss., and other synonyms), Chinese cultivars (*M. Toosenden* Sieb. & Zucc. and other synonyms), and Indian cultivars (numerous synonyms). Many of these names have been used in floras or to document phytochemical or other investigations into the biology of *Melia.* The two groups of cultivars originated in different parts of Asia through selection for desirable horticultural qualities.

Wild plants of *Melia Azedarach* occur in forests in an area including India and southern China, southward through the Indochinese Peninsula, parts of Malesia to New Guinea and tropical Australia, where they sometimes are large trees (to 40 m). Wild plants, which have larger leaflets (to 6 cm long) and smaller flowers, are evidently not hardy in cool-temperate regions. In contrast, plants naturalized or cultivated in temperate regions have smaller, serrate or lobed, usually glabrous leaflets and large bluish, pink, or white flowers. The chinaberry of the southeastern United States is presumably partly derived from plants introduced into Europe from the Middle East, which in turn are believed to have come at least as early as the 9th century B.C. from plants of Indian origin (Mabberley). Cultivars selected in Japan (from putative Chinese stocks) have been a second source of introductions into European and North American horticulture.

A name often applied to Mabberley's concept of wild plants of *Melia Azedarach* is *M. dubia* Cav.; flowering and fruiting specimens so-named in the herbarium of the Arnold Arboretum are markedly distinct from *Melia Azedarach* as it is represented in the Southeast. Mabberley has added *M. dubia* and several other names to the synonymy of *M. Azedarach,* citing his inability to correlate differences in flower color and leaf characters with geography. It would be interesting to know if the "wild" plants are reproductively isolated from those in cultivation, in view of the fact that hybrids are known among at least some of the cultivars.

Melia Azedarach is widely naturalized in Africa, and one or perhaps two other species appear to be indigenous to that continent. *Melia Bombolo* Welw. is reported from West Africa (Sénégal, Gabon, Democratic Republic of the Congo, and Angola; Staner & Gilbert) and *M. Volkensii* Guerke from tropical East Africa (Uganda; Gürke). The relationship between these species and *M. Azedarach* s. l. is unclear. The genus obviously needs monographic study.

The sole representative of the genus in the Southeast, *Melia Azedarach,* is reported to be polygamous on the basis of observations of trees growing in Taiwan (Lee, Styles (1972), family references). Individual cymules in an inflorescence are mostly three-flowered dichasia in which the terminal flower is perfect (and the first to open) and the two lateral flowers are staminate (and caducous following anthesis). Sometimes all three flowers are staminate. Perfect and staminate flowers are indistinguishable at anthesis, but the fate of individual flowers can be followed by observing the pattern of fruit set. My examination of herbarium specimens collected in the Southeast revealed that fruits are usually at the ends of pedicels that bear opposite scars (which represent the places where the staminate flowers were attached). Polygamy should be confirmed in our area by observations of plants in flower.

Plants of *Melia Azedarach* have many uses, although the species is not of great commercial importance. The wood has been used in cabinets, furniture, and cigar boxes, and in the manufacture of fiberboard. Pulp from the wood has been made into various kinds of paper in India. Styles & Khosla (family references) consider *M. Azedarach* to be a "species of enormous forestry potential," and report that a program to improve the species genetically is under way in Argentina.

A decoction of bark from the roots is reputed to be an effective vermifuge, probably reflecting the presence of vanillic acid (Chiang & Chang). Other parts of the plant are also used occasionally in folk medicine. The seeds contain about 40 percent oil. The endocarps are sometimes strung as beads, for example, in rosaries. A triterpenoid, azadirachtin, originally isolated from the fruits of *Azadirachta indica,* but also found in the fruit of *M. Azedarach* (Morgan & Thornton), inhibits feeding in desert locusts (*Schistocera gregaria*). Other kinds of insects are repelled by extracts of the plant. Fermented fruits of *M. Azedarach* were used as a source of alcohol during the American Civil War (Mabberley).

Fruits and leaves of *Melia Azedarach* are reported to be poisonous to humans and certain domestic animals (Carratala, Kwatra *et al.*). However, the poisonous principle has been elusive. A toxic alkaloid, tazetine, has been found in the bark and fruit (Morton, family references), and the presence of an alkaloid, azedarine, is mentioned by Carratala. The work of Morrison indicated that the toxicity of the fruit derives from an unidentified alkaloid, which acts in concert with a resin. However, Schulte and coworkers did not detect toxic substances in the fruits of *M. Azedarach.* Oelrichs and colleagues isolated four limonoids (meliatoxins) from the flesh of fruits from trees in Queensland. These proved toxic to pigs and mice in clinical trials.

Birds and fruit bats play a role in the dispersal of *Melia Azedarach* (White, 1986). In North America the robin (*Turdus migratorius migratorius*) is reported to eat quantities of the fruit (Beal, Elliott).

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Subfam. SWIETENIOIDEAE Harms in Engler & Prantl, Nat. Pflanzenfam. III. **4:** 267. 1896.

2. **Swietenia** Jacquin, Enum. Syst. Pl. Ins. Carib. 4, 20. 1760.

Small to large trees; bark dark brown, shallowly fissured; scales of terminal buds glabrous. Leaves even-pinnate (rarely odd-pinnate), apex of rachis aborting; young leaves with numerous scattered glandular hairs and a few long, simple hairs; leaflets petiolulate [or sessile], oblique at base, lower part of lamina of each narrower than upper, short [to long] acuminate, entire; leaflets usually deciduous before rachis. Plants monoecious; inflorescences borne on new growth; terminal flower of cymules carpellate, lateral flowers staminate. Flowers imperfect; perianth of staminate and carpellate flowers similar, calyx of 5 (rarely 4 or 6) nonoverlapping lobes, glabrous, margin uneven or ciliate; petals 5 (rarely 4 or 6), convolute in bud, entire or ciliate, otherwise glabrous. In staminate flowers the stamen tube urn-shaped, 10 (rarely 12)-toothed; anthers 10 (or 12), dorsifixed, inserted at a position below the stigma, alternating with the teeth; pollen spherical, ± psilate, margins of colpi thickened; ovary narrowly pyriform, (4)5(6)-locular, ovules rudimentary, style long, stigma narrower than

mouth of tube; nectariferous disc annular, obscurely lobed, extending slightly above the insertion of the ovary. In carpellate flowers stamen tube urn-shaped, anthers small and withered, inserted above the stigma, anthers and teeth of stamen tube ± flexed over stigma at anthesis, ovary globose, (4)5(6)-locular, each locule with numerous anatropous ovules in 2 rows; placentation axile; style short, stigma as broad as mouth of stamen tube, discoid, indistinctly 5-rayed, stigmatic surface on lower side; nectariferous disc annular, obscurely lobed, extending slightly above the insertion of the ovary. Fruit a 5-locular capsule, dehiscing septicidally from the base [or apex and base or from the middle to the ends], pericarp 2-layered, the woody outer layer separating first, 5-ridged columella persistent. Seeds large, in 2 rows, winged, attached by the funiculus near the apex of the axis; wing mostly elaborated from outer integument, weakly [or strongly] aerenchymatous at base and around seed; inner seed coat thin; embryo transversely elliptic, located at the bottom of the seed below the wing, radicle oriented perpendicularly to the long axis of the seed and to the position of the micropyle, cotyledons broader than long, plumule inconspicuous; endosperm very thin, inconspicuous, oily. TYPE SPECIES: *S. Mahagoni* (L.) Jacq., the only one included in the genus when it was established by Jacquin. (Named in honor of Gerard von Swieten, 1700–1772, Dutch physician and botanist, who worked in Vienna during the last third of his life and who was instrumental in the establishment of the botanic garden at Schönbrunn and the University of Vienna.]—MAHOGANY, CAOBA.

Three species of tropical and subtropical America; one, *Swietenia Mahagoni,* West Indian mahogany, native in our area only at the southern end of Florida (Monroe and Dade counties, including the Florida Keys), but hardy northward in Florida. Otherwise, it is indigenous to the islands of the western and northern Caribbean region (Greater Antilles, Bahamas) but evidently was introduced in Puerto Rico, the Virgin Islands, and the Lesser Antilles (Little; Little & Wadsworth, family references). However, the exact extent of its native range is not known because this species was planted extensively, probably beginning in the 1700's, and some populations represent escapes from cultivation. Indeed, this important tree has been introduced throughout the tropics as a source of timber and as a shade tree. It seeds freely, and isolated mature trees are sometimes surrounded by numerous seedlings, as, for example, in the Lesser Antilles (Howard).

Swietenia Mahagoni is allopatric with *S. macrophylla* King, Honduran mahogany, known from Mexico and Central America (Veracruz and Chiapas, Mexico, and Belize south to Panama) and South America (Colombia and Venezuela and disjunct to Peru, Bolivia, and Brazil), and *S. humilis* Zucc., restricted to the Pacific slope of Mexico (Sinaloa southward), Guatemala, Honduras, El Salvador, Nicaragua, and Costa Rica. *Swietenia macrophylla* and *S. humilis* are sympatric in parts of Mexico, Guatemala, and Costa Rica (Lamb, 1966; Styles in Pennington, 1981, family references), but detailed studies of co-occurring populations evidently have not been undertaken. Putative, spontaneous hybrids between open-pollinated trees of *S. macrophylla* and *S. Mahagoni, S. humilis* and *S. macrophylla,* and *S. humilis* and *S. Mahagoni* have

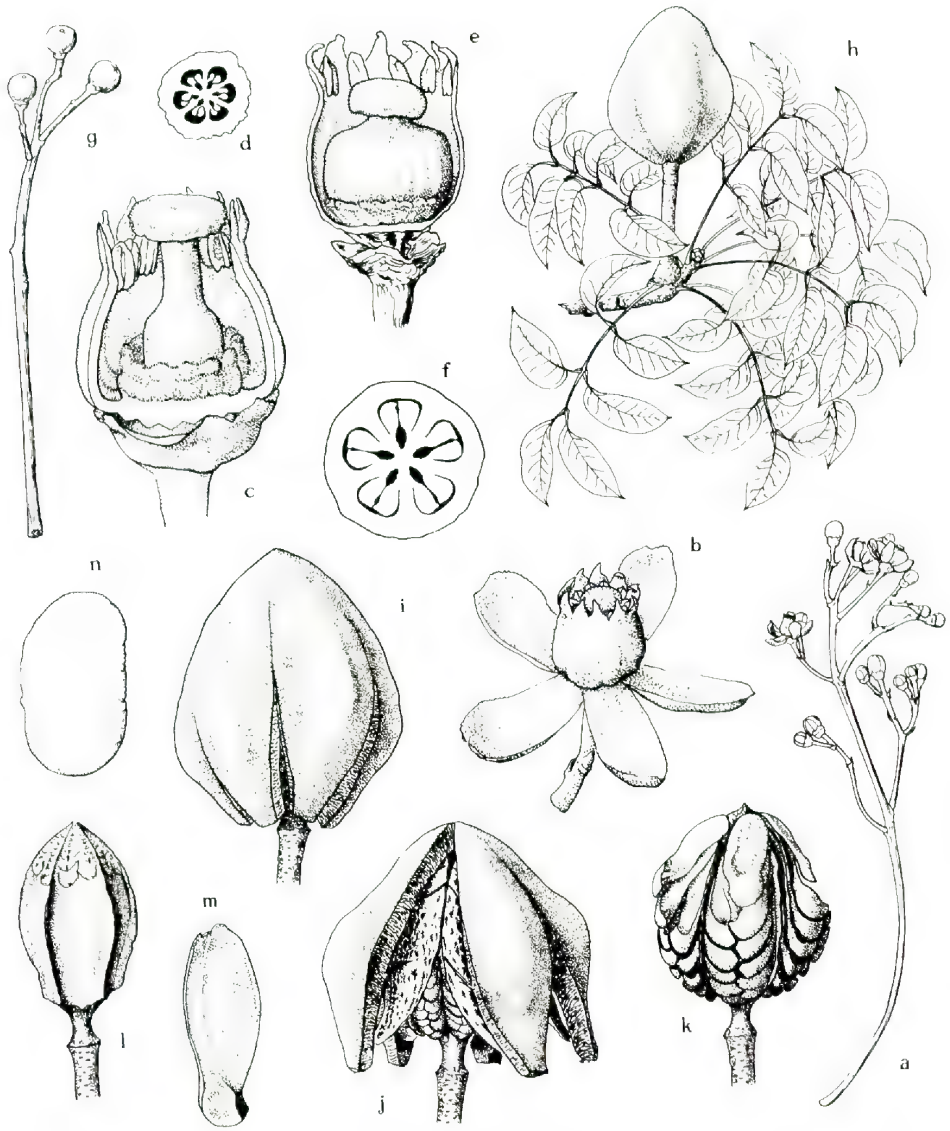

FIGURE 2. **Swietenia.** a–n, *S. Mahagoni:* a, inflorescence, × 1; b, staminate flower, × 5; c, same, with one sepal, petals, and part of staminal tube removed to show nectariferous disc and nonfunctional gynoecium, × 10; d, ovary of staminate flower in diagrammatic cross section, showing rudimentary ovules, × 12; e, carpellate flower with petals and part of staminal tube removed, showing gynoecium, disc, and rudimentary anthers, × 10; f, ovary of carpellate flower in diagrammatic cross section, showing ovules and placentation, × 12; g, inflorescence with very young fruit, and showing scars of staminate flowers, × 1; h, leafy branch with mature fruit, × ¼; i, j, stages in opening of fruit, × ½; k, axis of fruit (columella) with seeds after fall of woody valves, × ½; l, ridged columella with seeds removed, note two rows of scars, (cf. f), × ½; m, seed, × 1; n, embryo, oriented as in seed, radicle at left, cotyledon wider than long and extending above and below the position of radicle, cotyledons strongly coherent (second cotyledon not visible), × 2.

been recognized either in plantations of the parental species or in areas of sympatry (Whitmore & Hinojosa). The hybrids present various morphological traits that are intermediate between the parents, but detailed studies of progeny resulting from controlled crosses have not been undertaken to confirm these observations. Only in Taiwan have crosses between a tree of *S. macrophylla* (pollen parent) and *S. Mahagoni* been performed (Lee, 1968). The stomatal length to width ratio and leaflet size in the hybrid seedlings were in general intermediate between measurements of these features in seedlings from seeds produced through the self-pollination of flowers on the parental trees. Chromosome numbers of the plants used in this study were not determined.

The three species of *Swietenia* differ in a combination of traits, including vegetative, floral, and fruit characters. Leaflets in *S. Mahagoni* are generally smaller (mostly 4–6 cm long, 1.5–2.5 cm wide), petiolulate (especially the lower ones), and acute and sometimes aciculate (vs. mostly 7–9 cm long, 2–3 cm wide, subsessile, and long acuminate in *S. humilis* and mostly 9–13 cm long, 3–5 cm wide, petiolulate, and acute to short acuminate in *S. macrophylla*). *Swietenia Mahagoni* has the smallest capsules of the three species (4–6 cm long; vs. 8–16 cm in *S. humilis* and 12–15 cm in *S. macrophylla*) and also the smallest seeds. These are brown in contrast to the pale orange-brown seeds of *S. humilis* and the usually dark brown ones of *S. macrophylla*. The calyx and corolla are reported to be ciliate in *S. Mahagoni* and entire in *S. humilis* and *S. macrophylla* (Styles in Pennington, 1981, family references), but this difference was not apparent in numerous specimens of the three species that I studied. However, the flowers of *S. humilis* are slightly larger than those of the other two species (observations based on specimens in the combined herbaria of the Arnold Arboretum and Gray Herbarium). Although the diagnostic characteristics are largely quantitative and gradational, intermediates appear to be uncommon (except for the hybrids discussed earlier). Leaflet size and shape are variable in all three species, but especially so in *S. Mahagoni,* in which they can vary from two to four times longer than broad. Elliptic to ovate leaflets appear to be the commonest expression, although the shape is difficult to describe precisely because the laminae, and particularly the leaf bases, are asymmetrical, sometimes greatly so.

Swietenia and most other members of subfam. Swietenioideae have woody capsules containing a conspicuous columella and winged seeds. Species of *Swietenia* have ovoid woody capsules that open from the base to the apex (described by Johnson as starting in the middle of the capsule in *S. macrophylla*) and contain seeds with a large terminal wing, which is attached near the distal end of the columella. In *Khaya* A. Juss., the source of African mahogany and a genus thought by some (Lamb, 1966) to be close to *Swietenia,* the seeds have a complete, narrow marginal wing, and the capsules open from the apex to the base. Most other members of the tribe, except the poorly known *Schmardaea* Karsten, are restricted to the Old World.

Chromosome numbers vary within species (*Swietenia Mahagoni,* $2n = 12$, 18, 24, 36, 42, 46–48, 54, 60, 108) and between species (*S. macrophylla,* $2n = 54$ and *S. humilis,* $2n = 50$, 52, 56; Datta & Samanta, Khosla & Styles,

Styles & Vosa). The euploid series in *S. Mahagoni* was documented in plantation trees (Fiji Islands), and an additional number ($n = 28$) has been reported for a tree grown in India (Sareen & Kumar). These numbers indicate the existence of considerable karyological polymorphism, at least in plantation stock. Khosla & Styles counted $2n = 48$ (*S. macrophylla*), and $2n = 56$ (*S. humilis*) in plants obtained from within the native ranges of the species. The chromosome cytology of the genus is otherwise poorly known, particularly within naturally established populations.

Few detailed studies of the morphology of species of *Swietenia* have been undertaken. Lee (1967) was the first to show that the flowers of *S. Mahagoni* and *S. macrophylla* were either staminate (styles long, ovaries slender) or carpellate (styles short, ovaries globose). The trees are monoecious. The number of staminate and carpellate flowers per inflorescence is reported to vary, with staminate flowers being more abundant. Observations of the same tree over two years showed a large difference in the number of carpellate flowers formed on an annual basis. Pollen is released in sticky masses suitable for transport by insects, which presumably are attracted to the nectariferous disc. Flowers of *S. Mahagoni* and *S. macrophylla* are reported to be fragrant (Small; Lamb, 1966). Only the undersurface of the stigma is receptive to pollen (Tomlinson). Dichogamy may be the rule in members of subfam. Swietenioideae, including *Swietenia* (Styles, family references), since the sparse field observations indicate that the central carpellate flower of a three-flowered dichasium opens first, followed by anthesis of the staminate flowers, which occur in a pair below the carpellate flower. This asynchrony may promote outcrossing, but the hybridizations performed by Lee (1968) indicate that in *S. Mahagoni,* at least, the trees are self-compatible. Usually only one carpellate flower per inflorescence develops into a mature fruit.

Growth of *Swietenia Mahagoni* follows a pattern similar to one typical of temperate trees, namely, articulate monopodial branching, scaly terminal bud formation, and suppression of secondary branches on primary shoots during the first year and release of the branches during the second year (Tomlinson). The xylem anatomy of the West Indian and Honduran mahoganies has been thoroughly characterized (Rock; under family references see Kribs; Panshin; Record, 1919, 1941, 1944). Annual growth increments are demarcated by bands of parenchyma. In comparison with the wood of Spanish cedar (*Cedrela* spp.), another economically important timber tree in the Meliaceae, intervascular pits in the mahoganies are smaller in diameter (2–3 μm). In wood of the West Indian mahogany the perforation plates are simple, intervascular pitting of the vessel elements is alternate, pits of the fibers are simple and slitlike or vestigially bordered, and both apotracheal and paratracheal axial parenchyma are present, as are uniseriate and multiseriate heterocellular rays (Rock). Minute foliar nectaries occur on the petiole, rachis, petiolules, and both leaflet surfaces in all three species of *Swietenia* (Lersten & Rugenstein). Their positions in live plants are marked by minute glistening balls of nectar. Extrafloral nectaries such as these perhaps function to attract ants, which may help rid the plants of insect pests, a relationship demonstrated in other flowering plants. However, evidence for it in *Swietenia* is lacking.

The seed biology of *Swietenia* is poorly documented. Seeds of *S. macrophylla* and probably those of the two other species have a short (several month) period of viability after ripening, unless the seeds are dried to five percent moisture content (Lamb, 1966). Viability is prolonged with refrigeration. The seeds have a prominent wing, and this structure presumably facilitates dispersal by wind, even though seedlings may be abundant under or near large trees. Lamb (1966) reported that seeds from a large tree of *S. macrophylla* can be scattered on the leeward side over an area of about 10 acres, but Johnson notes that seeds of this species are rarely found more than 100 yards from the parent tree. Capsules are borne erect in *S. Mahagoni* (and the other species). The seeds are weakly attached to the columella (central axis) and remain hanging loosely in place after the capsule valves have fallen away, which happens in the winter in Florida (C. E. Wood, Jr., obs.). Seeds are presumably dislodged by gusts of wind. Abundant aerenchymatous tissue occurs at the embryo end and in the wing along the raphe in seeds of *S. humilis.* It may increase the buoyancy of the seed in the air or possibly help to keep the seed floating in water. Aqueous leachates of leaves of *S. Mahagoni* inhibit the germination of its seeds in the laboratory (Andorfer & Teas), suggesting a possible allelopathic effect in nature. Seedlings of both *S. Mahagoni* and *S. macrophylla* are cryptocotylar. In the former the eophylls are alternate, whereas in *S. macrophylla* they are opposite (Duke, 1965).

Swietenia Mahagoni was an important member of the highly diverse tropical hardwood forests that once were common in subtropical Florida (Craighead). Trees of the West Indian mahogany reaached a large size in hammocks (tree islands) that developed at places where the mineral soil or bedrock was slightly elevated (1 m or less) above the surrounding pinelands or glades (treeless wetlands). In such places fresh water remains year round in solution cavities and peat accumulates, both helping to maintain high humidity. West Indian mahogany was also common in a second kind of hammock that developed on ridges of marine marl deposited on the land by hurricane tides. Peat accumulation raised these low ridges further and isolated them from salt water. While charcoal preserved in the soil shows that fire swept through hammocks of both types, trees of *S. Mahagoni* can persist under such circumstances by forming root suckers.

Phoradendron rubrum (L.) Grisebach grows on *Swietenia* in some existing hammocks in Florida, and this parasite has been implicated in the death of larger trees on Key Largo and perhaps on Rhodes and Sand Keys (Cooley).

West Indian mahogany (*Swietenia Mahagoni*) and Honduran mahogany (*S. macrophylla*) are the sources of wood universally prized for cabinetry and fine woodworking for over 200 years. Honduran mahogany has been described as the "world's premier cabinet wood" and "perhaps the most valuable timber tree in the whole of tropical Latin America" (Styles in Pennington, 1981, family references; p. 400). Harvestable trees are still available in Mexico, Guatemala, and South America. West Indian mahogany is rare on the commercial market, and writing in the mid-1960's, Lamb commented that it had almost disappeared from commerce because the supply was exhausted. Its wood is thought to be superior to that of Honduran mahogany, which has a coarser grain and a less

rich color when finished. Both mahoganies are presently being grown in forest plantations. Under natural conditions *S. macrophylla* is reported to reach 60 m tall; trees of *S. Mahagoni* are generally shorter (to 20 m).

The wood of *Swietenia* came to the attention of Europeans early in the 1500's during the Spanish domination of the West Indies. Over the next century and a half mahogany was used in the West Indies for shipbuilding and repair and in the construction of buildings because of its great resistance to dry rot and termites and to warping when in contact with water. Spanish shipbuilders, first at Santiago, Cuba, and later at Havana Arsenal, Cuba, constructed many ships for the Spanish Navy using logs cut in Cuba and Mexico (Lamb, 1966). The use of mahogany for furniture in England began about 1715. It rapidly supplanted walnut and oak as the raw material for tables, chairs, and cabinets. Lamb named the period 1725–1825 the "golden age of mahogany," in reference to the development of furniture styles during that 100 years by English master craftsmen, including Thomas Chippendale, George Hepplewhite, and Thomas Sheraton, who based their innovative designs on the strength, durability, outstanding working qualities, and excellent finished color and luster that are characteristic of mahogany. American cabinetmakers were also using mahogany in Boston, New York, Philadelphia, and elsewhere during this period. Especially prized were boards with highly patterned grain. These came from the stumps, root crowns, and larger roots, as well as from logs that included the junction of the bole and a large branch. Such logs were sawed so that the boards had a Y-shaped grain pattern.

Overharvesting has eliminated large trees of West Indian mahogany throughout its range, and what little of its wood comes on the market is from plantation-grown trees. Trees of Honduran mahogany are still available in parts of Central and South America. However, many of the largest trees have been cut from accessible locations. Concern has been expressed about the severe depletion of potentially useful genetic stock for breeding purposes (Styles in Pennington, 1981, family references). Mahogany shoot borers, *Hypsipyla* sp. (Lepidoptera), are serious insect pests in many areas and have limited the development of mahogany plantations and the use of *Swietenia* species in reforestation projects (Styles & Khosla).

A decoction of the bark of *Swietenia Mahagoni* or of *S. macrophylla* has been used locally in the West Indies or Central America as a tonic and to treat inflamed mucous membranes and chest and other illnesses (Morton).

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HISTORY OF THE INTRODUCTION OF EXOTIC ELEMENTS INTO TRADITIONAL CHINESE MEDICINE

Shiu Ying Hu[1]

An investigation into the history of using products derived from introduced species of plants and animals in traditional Chinese medicine (TCM) clearly demonstrates East-West cultural interaction. The research was performed in a framework arbitrarily set with the time limited to before 1911 and the material included in three important references: *Zhong Yao Zhi* (*A New Chinese Materia Medica*; Anonymous, 1959–1961), *Zhong Yao Da Ci Dian* (*An Encyclopedia of Chinese Medicines*; Anonymous, 1977–1979), and *Zhong Cao Yao Xue* (*Chinese Pharmacology*; Anonymous, 1976–1980). The work contains a list of 94 commercial products arranged alphabetically by scientific name, together with the equivalent Chinese and English names; a chronological account of the first record of the species and imported products; an analysis of the reasons for using extra-Chinese elements in TCM; and an account of the principles and criteria for identifying exotic species.

When I began to study the medicinal plants of China in the early 1930's, the knowledge of Chinese materia medica was scattered in various ancient herbals (*ben-cao*). I prepared a list of Chinese plant esculents used for the conservation of health (*bupin*), and bought the products from groceries and Chinese drug stores in Guangzhou (Canton). I went to Luo-fou Shan in Guangdong repeatedly to learn about the sources of my collection of *bupin* from the monks and nuns residing in various Taoist temples and to collect voucher specimens with the help of the local herb collectors.

During the entire period of the Sino-Japanese War (1937–1945), I taught at West China Union University in Chengdu. Together with several senior students, I conducted a survey of the medicinal plants in the herb shops of the area (Hu, 1945). During summer vacations I went with colleagues and students to live in the villages of the Giarong tribe; we explored the vegetation and studied the lives of migrant collectors of crude drugs in the alpine meadows of Min Shan and Qiong-lai Shan in western Sichuan. Between September 1946 and March 1968 I was working on the Chinese collection in the herbarium of the Arnold Arboretum, and my interest in medicinal plants was overshadowed by taxonomic research and the duties of a professional botanist. In connection with field work for the preparation of a *Flora of Hong Kong,* I taught in the Biology Department of Chung Chi College, Chinese University of Hong Kong,

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Journal of the Arnold Arboretum **71:** 487–526. October, 1990.

between March 1968 and October 1975. At first only a few students in that university were interested in the study of local medicinal plants. We collected specimens from herbalists in the area, identified the species, and ascertained their uses. Later, my colleagues Y. C. Kong (Biochemistry Department), H. M. Chang, and J. Ma (both of the Chemistry Department) showed a growing interest in research on the chemical composition of various Chinese crude drugs. To check the efficacy of the medicines, they tested them on animals. They asked me to identify the specimens and to contribute some botanical descriptions. Gradually, under the leadership of Chang, the Chinese Medicinal Material Research Centre was organized in the Chinese University of Hong Kong. This institution grew fast. With a strong staff, advanced instrumentation, and the support of the University, local institutions, and individuals, it soon attracted the attention of scientists and scientific institutions from around the world. Its computerized information on traditional Chinese medicine (TCM) is linked with medical centers in London, Tokyo, and Washington. It is a worldwide bridge for disseminating knowledge of Chinese materia medica both past and present. In connection with this research center, my interest in Chinese medicinal plants was revitalized. This report is one of the results of subsequent studies.

The aim of this report is to provide a window through which historians of science can see the facts and the nature of material exchange and cultural diffusion between China and people in lands far and near. In addressing the questions, I began with the words what, when, where, why, and how about exotics used in TCM. A workable framework was arbitrarily formed by setting a time limit of 1911, the year when China was transformed from an empire to a republic, and by selecting three modern references: *Zhong Yao Zhi* (*A New Chinese Materia Medica*; Anonymous, 1959–1961), *Zhong Yao Da Ci Dian* (*An Encyclopedia of Chinese Medicines*; Anonymous, 1977–1979), and *Zhong Cao Yao Xue* (*Chinese Pharmacology*; Anonymous, 1976–1980). The comprehensive treatise of *An Encyclopedia of Chinese Medicines* contains 5767 entries of crude drugs from 4161 species of plants, 442 species of animals, and 58 kinds of minerals. For each plant entry, the accounts include the recognized Chinese name, its synonyms, the source material with scientific identification, a morphological description illustrated by a line drawing, notes on distribution and ecology, and information on cultivation (if the species is not wild), harvesting time, and procedure, identifying characteristics of the market product, chemical composition, pharmacology, special treatment needed before dispensing, properties, target organs and illnesses, selected recipes, and ancient references. The *Supplement* to this work (Anonymous, 1979) gives indexes to Chinese and scientific names and synonyms, Chinese and English equivalents of the chemical components, chemical formulas and properties, against pharmacological references, a classified list of diseases with cross references to remedies, a detailed bibliography for chemical composition, experimental and clinical reports for each entry, and three checklists for modern and ancient systems of measurements. Much of the information for this article is based on these references.

KINDS OF EXOTICS IN TCM

The exotics in a flora of a country are either cultivated plants or adventives fully established in the area. Volumes 1–4 of *Zhong Yao Zhi* (Anonymous, 1959–1961) and volumes 2 and 3 of *Zhong Cao Yao Xue* (Anonymous, 1976–1980) were carefully checked for extra-Chinese elements. Ninety-four commercial products prepared from 98 exotic species of plants and eight species of animals were selected. Several products are prepared from similar substances of different species. An alphabetic list of the botanical and zoological identifications of these crude drugs is given for quick reference, with the animal entries following those for plants (see TABLE 1). When a crude drug is prepared from two or more related species, the epithet of the primary source is listed first. Included in the enumeration are the Chinese and English names, the place of origin, and the date the item was first recorded in a Chinese herbal or pharmacopoeia.

In the list only five items (less than five percent) are of animal origin. These are ox bezoar, elephant hide and tusks, rhinoceros horns, and the ambergris of the sperm whale. Plant materials include 26 kinds of seeds, 18 leafy shoots, leaves, or whole herbaceous plants, 16 fruits, nine resins, six roots, six flowers, four fragrant woods, two extracts, one bark, and an exudate of a desert plant (alhagi). Botanically, these products are from plants belonging to 55 families of dicots and five of monocots. The largest contributing family is the Leguminosae, with 15 species in 11 genera. The Cruciferae and the Cucurbitaceae each contributes four species, while the Euphorbiaceae, Malvaceae, Umbelliferae, Styracaceae, Labiatae, Solanaceae and Palmae are each represented by three species. The Piperaceae, Burseraceae, Guttiferae, Flacourtiaceae, Combretaceae, Apocynaceae, Rubiaceae, and Compositae are each represented by two species, and the remaining 33 families have only one species each.

CHRONOLOGICAL ACCOUNT

It is an undeniable fact that man occupied the habitable continents and large islands long before his existence was recorded by ancient and/or modern explorers. Intentionally, man moved with his favorite animals and plants; unintentionally, weed seeds and parasitic animals traveled with him. Dogs and the paper mulberry (*Broussonetia papyrifera* (L.) L'Hér.) in Polynesia are good examples of the former; many garden weeds, of the latter. Several of the extra-Chinese elements used in TCM arrived in China in a similar fashion, some during prehistoric time. We have material evidence that hemp arrived in China during the Neolithic period. Broomcorn (*Panicum miliaceum* L.) and hemp (*Cannabis sativa* L.) were reported by Q. R. Wang and Guo (1980) from an archaeological site of a Neolithic community, carbon 14 dated at 4850 B.P. ± 180 years, on terraced land by Da-xia-he in Gansu. Archaeological evidence such as this is rare. For our purposes we have to use historical records to show the chronological sequence of the employment of exotic elements in TCM. Such records, however, should not be taken as the time of introduction, the exact date of which is unrecorded. Moreover, many ancient herbals and phar-

TABLE 1. **Exotics in Chinese Materia Medica.**

SCIENTIFIC NAME	CHINESE NAME[1]	ENGLISH NAME	PORTION USED	PLACE OF ORIGIN[2]	YEAR RECORDED (A.D.)
Abutilon theophrasti Medicus	Qing-ma (1)	Abutilon	Seeds	SW As	659
Acacia catechu (L.) Willd.	Er-cha (2)	Catechu	Extract	Tr As	1596
Alhagi pseudalhagi Desv.	Ci-mi (3)	Alhagi	Exudate	Mid E	739
Aloë barbadensis Miller	Lu-hui (4)	Aloe	Extract	Afr	973
Amomum krervanh Pierre & Gagnep.	Bai-dou-kou (5)	Siam Cardamon	Fruits	SE As	973
Andrographis paniculata (Burm. f.) Nees	Chuan-xin-lian (6)	Kiryat, creat	Whole plant	Tr As	?
Aquilaria agallocha Roxb.	Chen-xiang (7)	Aloeswood	Wood	SE As	540
Areca catechu L.	Bing-long (8)	Betel nut	Fruits	Tr As	1300
Benincasa hispida (Thunb.) Cogn.	Dong-gua-zi (9)	Winter gourd	Seeds	Tr As	100
Bombax ceiba L.	Mu-mian (10)	Tree cotton	Roots	SE As	1596
Boswellia carteri Birdw.	Ru-xiang (11)	Frankincense	Resin	Mid E	540
Brassica hirta Moench	Bai-jie-zi (12)	White mustard	Seeds	Eur	540
Brassica rapa L.	Yun-tai-zi (13)	Field mustard	Seeds	Eur	659
Bryophyllum pinnatum (L. f.) Oken	Lu-di-shen-gen (14)	Air plant	Whole plant	Afr	1848
Caesalpinia sappan L.	Su-mu (15)	Sappanwood	Heartwood	SE As	659
Canavalia gladiata (Jacq.) DC. &/or *C. ensiformis* (L.) DC.	Dao-dou (16)	Sword bean	Seeds, roots	Tr As	1596
		Jack bean	Seeds	WI	1596
Cannabis sativa L.	Hu-ma-ren (17)	Hemp seed	Fruits	SW As	100
Capsicum frutescens L.	La-jiao (18)	Red pepper	Fruits	Tr Am	1621
Carica papaya L.	Fan-mu-gua (19)	Papaya	Fruits	Tr Am	1848
Carthamus tinctorius L.	Hong-hua (20)	Safflower	Corollas	Med R	973
Cassia angustifolia Vahl &/or *C. acutifolia* Del.	Fan-xie-ye (21)	Senna	Leafy shoots	Tr As	1894
Cassia occidentalis L.	Wang-jiang-nan (22)	Coffee senna	Seeds	Tr As	1407
Catharanthus roseus (L.) G. Don	Chang-chun-han (23)	Madagascar periwinkle	Leafy shoots	Mad	1848
Cinchona ledgeriana Moens. &/or *C. succirubra* Pav.	Jin-ji-na-pi (24)	Quinine	Bark	S Am	1765
Citrullus lanatus (Thunb.) Matsum. & Nakai	Xi-gua-cui (25)	Watermelon	Young fruits	Afr	1596

TABLE 1. **Continued.**

SCIENTIFIC NAME	CHINESE NAME[1]	ENGLISH NAME	PORTION USED	PLACE OF ORIGIN[2]	YEAR RECORDED (A.D.)
Cleome gynandra L.	Bai-hua-cai (26)	Spider-wisp	Leafy shoots	Tr Am	1596
Commiphora myrrha Engler	Mo-yao (27)	Myrrh	Resin	Mid E	973
Coriandrum sativum L.	Yuan-sui-zi (28)	Coriander	Seeds	SW As	1061
Crocus sativus L.	Fang-hong-hua (29)	Saffron	Styles	Med R	1596
Cucumis melo L.	Tian-gua-zi (30)	Sweet melon	Seeds	C As	1061
Daemonorops draco Bl.	Xue-jie (31)	Dragon's blood	Resin	Indon	659
Dalbergia sissoo Roxb. &/or *D. parviflora* Roxb.	Jiang-chen-xiang (32)	Sissoo, fragrant rosewood	Heartwood	Tr As	756
Datura metel L.	Yang-jin-hua (33)	Datura	Flowers	Tr As	1596
Dryobalanops aromatica Gaertner	Bing-pian (Long-nao-xiang) (34)	Borneo camphor	Resin	Indon	659
Euphorbia antiquorum L.	Huo-yang-le (35)	Fleshy spurge	Stems	India	1848
Euphorbia lathyris L.	Qian-jin-zi (36)	Moleweed	Seeds	Mid E	973
Ferula assafoetida L.	A-wei (37)	Asafetida	Resin	C As	659
Ficus carica L.	Wu-hua-guo (38)	Fig	Fruits	Med R	1407
Foeniculum vulgare Miller	Xiao-hui-xiang (39)	Fennel	Fruits	Med R	659
Garcinia hanburyi Hooker f. &/or *G. morella* Desv.	Teng-huang (40)	Gamboge	Resin	SE As	756
Gomphrena globosa L.	Qian-ri-hong (41)	Globe amaranth	Flowers	Tr Am	1688
Gossypium herbaceum L. &/or *G. hirsutum* L.	Mian-hua-gen (42)	Upland cotton	Roots	Sw As	1596
Hordeum vulgare L.	Mai-ya (43)	Barley	Fruits	Sw As	540
Hydnocarpus kurzii Warb. &/or *H. anthelminthicus* Gagnep.	Da-feng-zi (44)	Chaulmoogra	Seeds	SE As	1536
Impatiens balsamina L.	Ji-xing-zi (45)	Garden balsam	Seeds	India	1407
Ipomoea nil (L.) Roth	Qian-niu-zi (46)	Morning glory	Seeds	Tr As	540
Isatis tinctoria L.	Da-qing-ye (47)	Woad	Leaves	Eur	1061
Kochia scoparia (L.) Schrader	Di-fu-zi (48)	Summer cypress	Seeds	Med R	100
Lablab purpureus (L.) Sweet	Bai-bian-dou (49)	Hyacinth bean	Seeds	Med R	540

TABLE 1. **Continued.**

SCIENTIFIC NAME	CHINESE NAME[1]	ENGLISH NAME	PORTION USED	PLACE OF ORIGIN[2]	YEAR RECORDED (A.D.)
Lantana camara L.	Ma-ying-dan (50)	Lantana	Flowers, roots	Tr Am	1848
Lawsonia inermis L.	Zhi-jia-hua (51)	Henna	Leaves	Med R	300
Liquidambar orientalis Miller	Su-he-xiang (52)	Storax	Resin	As M	547
Linum usitatissimum L.	Hu-ma-zi (53)	Flax	Seeds	Euras	100
Luffa aegyptica Miller	Si-gua-luo (54)	Sponge gourd	Fiber of fruit	Tr As	1596
Mimosa pudica L.	Han-xiu-cao (55)	Sensitive plant	Whole plant	Tr Am	1848
Mirabilis jalapa L.	Zi-mo-li (56)	Four-o'clock	Roots	Tr Am	1708
Myristica fragrans Houtt.	Rou-dou-kou (57)	Nutmeg	Seeds	Indon	973
Nerium oleander L.	Jia-zhu-tao (58)	Oleander	Leafy shoots	Med R	1688
Nicotiana tabacum L.	Yan-cao (59)	Tabacco	Leaves	Tr Am	1624
Ocimum basilicum L.	Luo-le (60)	Sweet basil	Leafy shoots	Tr As	1061
Opuntia dillenii Haw.	Xian-ren-zhang (61)	Prickly pear	Fleshy stems	Tr Am	1848
Panax quinquefolius L.	Xi-yang-shen (62)	American ginseng	Roots	EN Am	1757
Papaver somniferum L.	Ying-su-ke (63)	Opium poppy	Fruits	As M	973
Phoenix dactylifera L.	Hai-zao (64)	Date	Fruits	Med R	300
Piper longum L.	Bi-ba (65)	Long pepper	Young fruits	Tr As	973
Piper nigrum L.	Hu-jiao (66)	Black pepper	Fruits	Tr As	659
Pistacia vera L.	Wu-ming-zi (67)	Pistachio	Seeds, bark	SW As	739
Pogostemon cablin (Blanco) Bentham	Guang-huo-xiang (68)	Patchouli	Leafy shoots	Philip	1061
Populus diversifolia Schrenk &/or *P. euphratica* Oliver	Hu-tong-lei (69)	Amber	Resin	Mid E	890
Portulaca oleracea L.	Ma-chi-xian (70)	Purslane	Whole plant	Tr Am	934[3]
Prunus dulcis (Miller) D. A. Webb	Bian-he-tao (71)	Almond	Seeds	SW As	739
Psidium guajava L.	Fan-shi-liu (72)	Guava	Leafy shoots	C Am	1848
Psoralea corylifolia L.	Bu-gu-zhi (73)	Bauchee seed	Seeds	India	973
Punica granatum L.	Shi-liu (74)	Pomegranate	Fruits	As M	540
Quisqualis indica L.	Shi-jun-zi (75)	Rangoon creeper	Seeds	SE As	973
Raphanus sativus L.	Lai-fu (76)	Radish	Seeds, roots	Med R	659
Ricinus communis L.	Bi-ma-zi (77)	Castor bean	Seeds	Afr	659

TABLE 1. **Continued.**

SCIENTIFIC NAME	CHINESE NAME[1]	ENGLISH NAME	PORTION USED	PLACE OF ORIGIN[2]	YEAR RECORDED (A.D.)
Rosmarinus officinalis L.	Mi-die-xiang (78)	Rosemary	Leafy shoots	Med R	739
Ruta graveolens L.	Yun-xiang (79)	Rue	Leafy shoots	Med R	273
Santalum album L.	Tan-xiang (80)	White sandalwood	Wood	Indon	540
Saussurea lappa (Dcne.) C. B. Clarke	Guang-mu-xiang (81)	Puchok, costusroot	Roots	Kashmir	100
Scaphium scaphigerum (G. Don) Guib. & Planchon	Pang-da-hai (83)	Pungtalai	Seeds	Tr As	739
Sesamum orientale L.	Hei-zhi-ma (82)	Sesame	Seeds	Afr	100
Strychnos nux-vomica L.	Ma-quian-zi (84)	Nux vomica	Seeds	Tr As	1596
Styrax benzoin Dryand &/or *S. benzoides* Craib. or *S. tonkinensis* Craib.	An-xi-xiang (85)	Sumatran benzoin; Siam benzoin	Resin	SE As	659
Syzygium aromaticum (L.) Merr. & Perry	Ding-xiang (86)	Cloves	Flower buds	Indon	973
Tamarindus indicus L.	Suan-jiao (87)	Tamarind	Fruits	Afr	1370
Terminalia chebula Retz.	Ke-zi (88)	Myrobalan	Seeds	India	659
Trigonella foenum-graecum L.	Hu-lu-ba (89)	Fenugreek	Seeds	Med R	1061
Bos taurus Gmelin	Niu-huang (90)	Ox bezoar	Gallstones	India	1848
Elephas maximus L.	Xiang-pi (91); Xiang-	Elephant	Hide, tusks	Tr As	1596
Physeter catodon L.	Long-yang (93)	Sperm whale	Ambergris	Indon	1228
Rhinoceros unicornis L.	Xi-jiao (94)	Rhinoceros	Horns	Tr As	100
R. sondaicus Desmarest &/or *R. sumatrensis* Cuvier		Rhinoceros	Horns	Indon	100
R. bicornus L. &/or *R. simus* Cottoni		Rhinoceros	Horns	Afr	1840

[1] The numbers in parentheses in this column correspond to the numerical sequence of Chinese idiograms provided in APPENDIX I.

[2] The abbreviations used are: Afr = Africa, As M = Asia Minor, C As = Central Asia, EN Am = Eastern North America, Eur = Europe, Euras = Eurasia, Indon = Indonesia, Mad = Madagascar, Med R = Meditterranean Region, Mid E = Middle East, Philip = Philippines, S Am = South America, SE As = Southeast Asia, SW As = Southwest Asia, Tr Am = Tropical America, Tr As = Tropical Asia, WI = West Indies.

[3] A native of the New World, this species was evidently dispersed to the Old by natural means, most likely through the dispersal of its dustlike seeds in storms that transported them to the upper atmosphere. This would explain its presence in TCM before Columbus had discovered the New World.

macopoeias are not properly dated, with some of them indicating just the reign of a certain emperor. The information traced from such records can only be broken down into broad categories of particular Chinese dynasties: the Han Dynasty and before, the Three Kingdoms Epoch, the North-South Division Epoch, the Tang Dynasty, the Song Dynasty, the Yuan Dynasty, the Ming Dynasty, and the Qing Dynasty. The designation of dynasty and epoch follows the chart given in the revised American edition of *Mathews' Chinese-English Dictionary* (see Mathews, 1972).

In the following explanations of the introduction of extra-Chinese elements, the romanization of the authors and the references follows the *New China Dictionary* (*Xin-hua Zi-dan*), hyphenated for the convenience of readers who do not know Chinese. The phrase *ben-cao* appears in many of the herbals and pharmacopoeias. This term has been translated as "materia medica." From the Tang Dynasty onward, many *ben-cao* were prepared under imperial orders. Publications sponsored and supported by the central government, and those prepared by individuals approved by the emperor, are here translated as "pharmacopoeias." Ancient Chinese herbals were hand-copied. Many of them were lost, others were changed by later workers with the original authorship retained to lend authority, and still others were incorporated into later works, giving credit to the original writers. Li Shi Zhen (1597) was the finest author of the third type. In his *Ben-cao gan-mu,* he first incorporated all known ancient records for each item entry, giving the name of the authors, and then adding his own observations and discoveries. The following account on the dating of the earliest records of the extra-Chinese elements in TCM represents a digest from Li (1597), *Zhong Yao Zi* (Anonymous, 1959–1961), and *Zhong Yao Da Ci Dian* (Anonymous, 1977–1979). These herbals and their respective authors have been included in the literature cited for this paper. For each entry an English translation of the title is followed by a pin-yin romanization, and as much pertinent publication information has been added as possible. These historical documents are available in research libraries in North America such as the collections of the Library of Congress and the Yenching Library at Harvard University. To assist scholars familiar with Chinese, a numerical list of Chinese idiograms for these titles is presented in APPENDIX II. The number of each reference in APPENDIX II follows the reference in the LITERATURE CITED section of this paper.

HAN DYNASTY AND BEFORE (B.C. 206–A.D. 200)

The first record of Chinese medicinal material is the *Herbal Classics of the Divine Plowman* (Shen-nong ben-cao jing). This work represents a crystallization of the empirical knowledge of the prehistoric and early historical people of China about the healing efficacy of natural objects (plants, animals, water, earth, and minerals). The authorship is not known, but it is attributed to Shen-nong, a mythological figure who is said to have tried hundreds of kinds of plants, to have used himself as an experimental subject, to have been poisoned three times daily, to have been saved, and to have learned how to help the

people in their healthcare through his experiences. In this account, the exotic elements recorded included *Benincasa hispida, Cannabis sativa, Kochia scoparia, Linum usitatissimum, Saussurea lappa, Sesamum orientale,* and *Rhinaceros unicornis.*

Three Kingdoms and Western Jin Epochs (A.D. 200–300)

During this period there were two persons who wrote about their experiences in South China, where they had encountered Arabian traders with unusual objects. In *Collections of a Man of Peace* (Zi-an ji) Sima Sui (A.D. 231–273) mentioned that *Ruta graveolens* was used for keeping silverfish from books. Ji Han (A.D. 263–306) in *A Description of Plants of the South* (Nan-fang cao-mu Zhuang) recorded *Phoenix dactylifera* and *Lawsonia inermis,* introduced by Arabian merchants, and *Areca catechu,* from tropical Asia.

North South Division Epoch (A.D. 425–590)

The first increase in recorded knowledge of Chinese materia medica occurred during this period. The outstanding recorder was Tao Hong-jing, a native of southern Jiangsu Province. He was a well-educated person who refused to serve the government, preferring to retreat into the mountains to learn from the people of their experiences in preserving life. He considered that by leading this type of life, he could achieve the manifestation of the heart of the sages in the service of the people. He prepared two treatises on materia medica, *Unrecorded Materials of Eminent Physicians* (Ming-yi bie-lu) and *A Commentary on Shen-nong's Herbal Classics* (Shen-nong ben-cao jing ji-zhu). In the second work, he incorporated his findings of *Unrecorded Materials of Eminent Physicians* into a copy of Shen-nong's Herbal, using red ink for the information taken from Shen-nong's Herbal and black ink for his additions. Tao's work was quoted repeatedly by Li Shi-zhen. *Aquilaria agallocha, Boswellia carteri, Brassica hirta, Lablab purpureus, Punica granatum,* and *Santalum album* were recorded by Tao.

Tang Dynasty (A.D. 618–905)

Emperor Gao-zong ascended the throne in A.D. 650. He was concerned with having a complete pharmacopoeia and appointed the Minister of Works, Li Chi, to revise Tao's *Commentary on Shen-nong's Herbal Classics.* The complete work consisted of seven volumes and is known as *Duke Ying's Tang Pharmacopoeia* (Ying-gong Tang ben-cao). A decade later, Su Gong pointed out the need for a revision of this pharmacopoeia. The Emperor appointed a team of 22 persons to cooperate with Su Jing. The complete work, the *New Tang Pharmacopoeia* (Tang ben-cao), consisted of 53 volumes with illustrations. The extra-Chinese elements in this work were *Abutilon theophrasti, Brassica rapa, Caesalpinia sappan, Daemonorops draco, Dryobalanops aromatica, Ferula assafoetida, Foeniculum vulgare, Piper nigrum, Raphanus sativus, Ricinus communis, Styrax benzoin,* and *Terminalia chebula.* In the Tang Dynasty, Japan and Korea had diplomatic relations with China. Soon after

this work was completed, it was copied and carried by returning students and/or diplomatic or Buddhist missions to those countries.

Several individuals interested in the materia medica of China did independent research on the subject. Chen Cong-qi completed the *Unrecorded Materia Medica* (Ben-cao shi-yi) in A.D. 739. He was a critical worker and added approximately 400 items not mentioned in the *New Tang Pharmacopoeia.* These additions were quoted by Li Shi-zhen. The extra-Chinese material included in Chen's work were *Alhagi pseudalhagi, Pistacia vera, Rosmarinus officinalis,* and *Scaphium scaphigerum.*

By the middle of the eighth century, the first materia medica of subtropical and tropical China and adjacent areas of the Indo-Malayan Peninsula appeared. This was Li Xun's *A Register of the Medicine Imported via the Seas* (Hai-yao ben-cao), completed in A.D. 756. Li's grandfather was an Arab with a successful spice and medicine trade; he resided partially in Guangzhou, then known as Nan-hai. His riches brought him such fame and honor that he was elevated to share the surname of the imperial family, Li, during the Tang Dynasty. With this background, and knowing the family business, Li Xun was qualified to write on the imported medicines that came from the South Seas. In this work, a product prepared from *Garcinia hanburyi* or *G. morella,* Teng-huang, was first mentioned.

By the close of the Tang Dynasty, an officer of the imperial government wrote about the strange things he saw beyond the Nanling Range. Liu Xun, in his *Records of Strange Articles* (Ling-biao lu yi, A.D. 889, 890), recorded a resin called tears of the Arabian tong (Hu-tong lei) and an almond that he described as a peach with a compressed kernel, both of which were seen in the homes of the Arabian traders. He gave a vivid description of the almond, saying in Chinese that this kind of peach was cultivated not for the flesh, but for the compressed kernels with thin shell that tasted like the seed of the northern peach; one end of the compressed kernel is round, and the other is pointed. These articles are products of *Populus euphratica* and *Prunus dulcis,* respectively.

SONG DYNASTY (A.D. 960–1200)

In the history of Chinese materia medica, the Song Dynasty could be considered the Golden Era for the publication of pharmacopoeias. The first Emperor, Tai-zu, appointed the Imperial Pharmacist, Liu Han, and a Taoist monk, Ma Zhi, to lead a team of nine in revising the Tang pharmacopoeia. Using the works written during the Tang Dynasty as references, they organized the material, placed many former names into synonymy, and added 133 new items. It took them seven years to complete the revision, which filled 21 volumes, with the accounts from *Shen-nong ben-cao* written in white ink and all other references in black ink. This work is known as the *Pharmacopoeia of the Kai-bao Reign* (Kai-bao ben-cao, A.D. 973). Exotic elements recorded were *Aloë barbadensis, Amomum krervanh, Carthamus tinctorius, Commiphora myrrha, Euphorbia lathyris, Myristica fragrans, Papaver somniferum, Piper longum, Psoralea corylifolia, Quisqualis indica,* and *Syzygium aromaticum.*

In A.D. 1058 the fourth emperor, Ren-zong, had the imperial medical team, headed by Zhang Yu-xi and Lin Yi, revise the 100-year-old *Pharmacopoeia of the Kai-bao Reign.* The working team added 82 new items and revised 17 entries. Known as the *Revised Pharmacopoeia of Gia-you Reign* (Gia-you bu-zhu shen-nong ben-cao, A.D. 1061) the work consists of 20 volumes. The new exotics were *Coriandrum sativum, Cucumis melo, Isatis tinctoria, Ocimum basilicum, Pogostemon cablin,* and *Trigonella foenum-graecum.* Emperor Ren-zong also issued a decree ordering officers of all the states and counties to prepare illustrations of their native natural objects used for healing purposes. On gathering the drawings, the Emperor appointed Su Song to prepare descriptions and to be the editor of the new work, which consists of 21 volumes and is known as *An Illustrated Pharmacopoeia* (Tu jin ben-cao, A.D. 1062). This work has been quoted by all subsequent authors dealing with Chinese materia medica.

In A.D. 1108, the second year of the Da-guan Reign, Emperor Hui Zong received a manuscript on materia medica prepared by Tang Shen-wei, a practitioner from Sichuan Province. In this manuscript, Tang modified the text of the *Revised Pharmacopoeia of Giao-you Reign* and incorporated the illustrations from *An Illustrated Pharmacopoeia.* To this combined work he added prescriptions and notes for dietary applications to each entry. He titled the manuscript *Verified Identification of Materia Medica* (Zheng-lei ben-cao). The Emperor accepted the manuscript, which then became known as the *Pharmacopoeia of the Da-guan Reign* (Da-guan ben-cao). In this work the fragrant woods of *Dalbergia sissoo* and *D. parviflora* were first mentioned.

Sinologists have characterized the Tang (A.D. 618–905) and the Song dynasties as the grand period of growth of Chinese culture. Contacts with nations far and near were frequent. Members of religious expeditions and diplomatic missions to India and southeastern Asia learned to use things unfamiliar to them, and they frequently brought samples and/or propagules back to China. Soldiers in war and traders in peace brought exotic things from nations near. With regard to the extra-Chinese elements used in TCM, the nature of the items recorded during the Tang Dynasty is very different from those of the Song Dynasty. In the Tang period medicines, food, spices, and resins and dyes, each with 25 percent of the total, comprised the material record. In the Song Dynasty the number of fragrant woods increased very prominently, consisting of one-half of the newly recorded exotics. During the Song Dynasty the central government supported the preparation of pharmacopoeias and evidently also encouraged the importation of fragrant woods and spices; furthermore, it established a Bureau of Spices and Medicines to oversee their importation. The reason for such governmental efforts will be explained below.

Yuan Dynasty (A.D. 1206–1368)

Historians often characterize this period as China under the Mongols. Although there was much communication and exchange of materials and ideas between the West and the East, very few new exotics were added to the Chinese materia medica. Practitioners of the Yuan Dynasty simply followed tradition,

used the phamacopoeias of the Sung Dynasty, prepared their prescriptions, and carried on with their business. Near the end of the Yuan Dynasty, Zhu Zhen-heng prepared *A Supplement to Herbal Commentaries* (Ben-cao yan-yi bu-yi, A.D. 1358). In this work chaulmoogra (Da-feng-zi—*Hydnocarpus kurzii* and/or *H. anthelminthicus*) was first recorded.

MING DYNASTY (A.D. 1368–1644)

Countries such as Japan and Korea shared the heritage and information on Chinese medicine from the herbals and pharmacopoeias prepared in the Han, Tang, and Song dynasties. The Western World learned about Chinese medicine through the materia medica completed in the Ming Dynasty, particularly from Li Shi-zhen's *Materia Medica with Commentaries* (Ben-cao gang-mu, 1596). Unlike the works completed during the Tang and Song dynasties, those done during the Ming Dynasty were realized through individual interests and efforts. Five treatises dealing with exotic elements used in TCM are discussed here.

The *Materia Medica of Southern Yunnan* (Dian-nan ben-cao, A.D. 1370), by Lan Mao, contained *Tamarindus indicus. Famine Herbal* (Jiu-huang ben-cao, A.D. 1407), by Zhu Xiao, included *Cassia occidentalis, Ficus carica,* and *Impatiens balsamina.* Ni Zhu-mo, in *Organized Collections of Materia Medica* (Ben-cao hui yan, A.D. 1624), first recorded tobacco (*Nicotiana tabacum*), introduced primarily for smoking, but in recent years rural people in Fujian have used it in the preparation of a poultice, which is mixed with rice gin to treat breast cancer.

Li Shi-zhen, after failing the qualifying examinations for governmental officers, entered the second-best profession of the time, becoming a practitioner in medicine. With his knowledge of the Chinese classics and his practical experience in diagnosing illnesses and prescribing remedies, he prepared a manual for practitioners of traditional Chinese medicine, Ben-cao gang-mu. When Li used *gang* and *mu,* he implied arrangement and classification. From the approximately 800 references, he selected 1518 items; he also provided 374 new entries. For each of the 1892 objects, he gave a recognized name, which he called *gang,* and cited all the synonyms with his commentaries, which he called *mu.* To such a framework, he added information on properites, tastes, and efficacy against illness, as well as recipes. In his treatment the new extra-Chinese elements were *Acacia catechu, Bombax ceiba, Canavalia ensiformis* or *C. gladiata, Citrullus lanatus, Cleome gynandra, Crocus sativus, Datura metel, Gossypium hirsutum, Luffa aegyptica, Strychnos nux-vomica,* and the hide and tusks of *Elephas maximus.*

During the Ming Dynasty, a famous treatise on plants and agriculture, *Monograph of Flowers* (Qun fang pu, A.D. 1621) was published by Wang Xiang-jin. In this work *Capsicum frutescens* was first recorded.

QING DYNASTY (A.D. 1644–1910)

Information on the exotic elements used in TCM before the Qing Dynasty was recorded largely in ancient herbals or pharmacopeias. During the Qing Dynasty both the elements employed and the source references changed. The

major portion of the information was recorded in treatises on horticulture and agriculture. The first such work was the famous *Flower Mirror* (Mi-chuan hua jing, A.D. 1688), by Chen Hua-zi. *Gomphrena globosa* and *Nerium oleander* were recorded in this work. *Mirabilis jalapa* first appeared in *Enlarged Monograph on Flowers* (Guang qun fang fu, A.D. 1708), by Liu Hao. Wu Yi-lo, in his *Newer Version of Materia Medica* (Ben-cao cong xin, A.D. 1757), first mentioned *Panax quinquefolius.* Zhao Xue-min, in his *Supplement of Ben-cao Gang Mu* (Ben-cao gang mu shi-yi, A.D. 1765) included quinine (*Cinchona succirubra* or *C. ledgeriana*), and ambergris from *Physeter catodon.*

The most outstanding work containing comprehensive information on the botany of China, *An Illustrated Treatise on Plants* (Zhi-wu ming shi tu kao, A.D. 1848), was prepared by Wu Qi-zhung. The extra-Chinese elements included in this treatise were *Bryophyllum pinnatum, Carica papaya, Catharanthus roseus, Euphorbia antiquorum, Lantana camara, Mimosa pudica, Opuntia dillenii, Psidium guajava,* and the gallstones of *Bos taurus.*

Belated Records

Two extra-Chinese elements commonly used in TCM before they were recorded in herbals or botanical treatises are creat (*Andrographis paniculata*), and senna (*Cassia angustifolia* or *C. acutifolia*). Evidence of their introduction into China during the Qing Dynasty is convincing for creat and tangible for senna.

Andrographis paniculata, a common weed in hedgerows throughout the plains of India, Bangladesh, and Burma, has been used locally in those countries in ethnomedicine for hundreds (thousands) of years. Some authors recorded it as an annual because it flowers during the first years of its life cycle. In the tropics new shoots emerge from the old plant after the dry season, and eventually the plant appears shrubby. I have seen the species growing in similar habitats in Hong Kong, flowering and fruiting the first year as an herb and growing as a perennial shrub in undisturbed sites.

Andrographis paniculata has been reported from northern India southward to Sri Lanka and eastward to Java. George Watt (1889) reported over two dozen vernacular names for the species, including kiryat (Hindi), kalmegh (Gengali), kiriyatta (Malay), kirata (Sanskrit), and qasabhuva (Arabic), from that vast area and cited its ethnomedical properties as a febrifuge, stomachic, tonic, alterative, and anthelmintic. As a bitter tonic, stomachic, and febrifuge, the herb has been shared and spread by ethnic people throughout tropical Asia but has been unrecorded until recently. Its widespread use and cultivation in northern China is modern, but its actual introduction must have been prior to 1932, when it was mentioned in *Records of Gathering Medical Herbs in South China* (Ling-nan cai-yue lu, Xiao, 1932).

From both the ethnobotanical practices and the vernacular names, it seems that *Andrographis paniculata* was introduced by the ethnic people living in the mountains of northern India, Balgadesh, Burma, and southern China. In the Bengal region the expressed juice of the leafy shoots is mixed with cardamon, cloves, and cinnamon, dried in the sun into small pills called alui, and used

to treat children for colic, loss of appetite, and irregular stools, and adults after a fever and for advanced stages of dysentery and general debility. Watt gave additional information that creat leaves mixed with the pulp of ripe tamarind were carried by wandering doctors as an antidote to the venom of poisonous snakes. The tribes in the mountains of Guangxi and Guangdong also used *A. paniculata* for fever, dysentery, and snake bite.

Senna is a popular purgative in southern Asia. Its laxative principles are two glycosides, sennoside A and sennoside B. The commercial product consists of the dried leafy shoots of *Cassia acutifolia,* indigenous to northern Africa, and *C. angustifolia,* native to Yemen and southern Arabia. Dealers called the product from *C. acutifolia* Alexandrian senna, and that from *C. angustifolia* Arabian senna. Both species are cultivated in India, the source area of the senna imported into China, and both are shrubs 1 m tall with lanceolate leaves.

Historically, senna was introduced by the Arabs to India, where the species has been extensively cultivated. We have no record of its introduction by the Arabs into China. This could have been because Chinese herbal medicine had a better and more effective purgative, rhubarb (da-huang, *Rheum officinale* Baillon and *R. palmatum* L.), which was widely accepted by the people before the arrival of the Arabian traders. Consequently, the Arabs were unable to create a market for senna in China. This situation continued until the industrialized European countries forced China to open her ports for international business. According to records in the list of Chinese medicines prepared under the instruction of the British Inspector General of Customs, Robert Hart, for the China Imperial Maritime Customs Department (see Anonymous, 1889), senna entered China by sea via India and Japan and overland through Yunnan-Sichuan.

Effect of Time on the Nature of Extra-Chinese Elements

The chronological account of the recorded exotics used in TCM reveals several unique characteristics. First, they were obviously introduced into China a very long time ago. The record made about the beginning of the Christian era (*Herbal Classics of the Divine Plowman*) shows that seven exotics were already in use in Chinese medicine. Two of these items, puchok (root of *Saussurea lappa*) and the rhinoceros horn, were imported overland from India. The remaining five substances were obtained from plants that were spread in association with adventurous prehistoric and/or ancient people who traveled extensively by the means of their time. Hemp arrived in China almost 5000 years ago in association with Neolithic man.

The second outstanding characteristic is the continuous growth in the number of exotics, with gradual changes in what was imported. When the data are plotted in a simple graph (see Figure 1), the growth in number of exotics used in TCM becomes very obvious. Each point in the graph represents the accumulated number of exotics used in TCM at that particular time. The model is meaningful only when an item is used continuously from the time of its introduction. This condition is true with all the recorded exotics listed here because they are still in common use.

The change in the nature of the exotics becomes obvious after an analysis

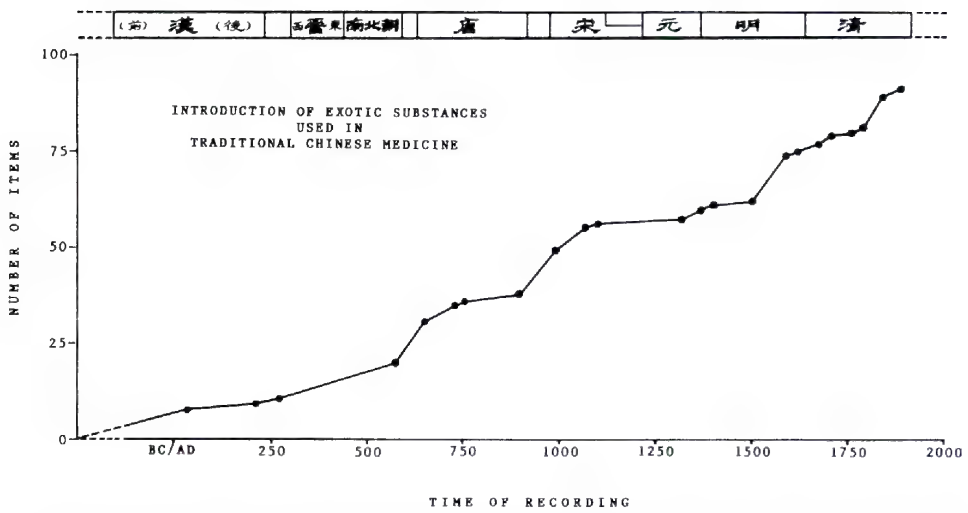


FIGURE 1. Increase in number of exotics used in TCM. Broken lines indicate time before and after period investigated in this study.

of their general function. Five of the earlier-mentioned seven items recorded from the Han Dynasty were from plants introduced primarily for daily necessities—that is, for food and fiber. There was only one substance among them, mu-xing (dried root of *Saussurea lappa*), that was imported as an aromatic medicine. At that early date, aromatic material comprised about 14 percent of the total imports. The increase in the proportion of aromatic products is very obvious. In the North-South Division Epoch, spices and aromatic materials were 37 percent of the total recorded items, in the Tang Dynasty 41 percent, and in the Song Dynasty 54 to 61 percent. The growth in exotic fragrant-wood species and aromatic substances reached a peak in the Song Dynasty due to the encouragement of the central government. During that period the State Department established a Bureau of Spices and Aromatic Medicine to deal with gifts and tributes of various diplomatic missions; the officers made requests and suggestions of articles to be brought into China in exchange for precious Chinese materials. In the Ming and Qing dynasties there was an obvious change of direction in importation. Substances for comfort and enjoyment of life other than spices and aromatic materials were brought in. Tobacco was recorded in the middle Ming, and cotton in the late Ming. Both these plants became extensively cultivated, one as a fumitory and the other for fiber. Their uses in medicine were secondary. During the Ming and Qing dynasties, introduction of plants for ornamental purposes increased very fast, from 27 percent of Ming importations to 50 percent of Qing records. New plants introduced for food comprised 18 percent of the species recorded in both the Ming and Qing dynasties.

The third prominent feature of the exotic elements used in TCM is the effort made toward self-sufficiency in the supply of these materials. Of all the plant products, 70 percent of the species have been cultivated as important field crops in China, two thirds of these for food, fiber, and ornamentals and one third for medicine. Six of the exotic elements are adventive species that have

TABLE 2. **Source areas and number of items.**

PLACE OF ORIGIN	NUMBER OF SPECIES		
	Plants	**Animals**	**Total**
Tropical Asia	14	1 + 1*	14 + 1*
Mediterranean Region	14	0	14
Tropical America	13	0	13
Southeast Asia	8	0	8
Southwest Asia	5	0	5
Middle East	7	0	7
Africa	5	1	6
Indonesia	5	1 + 1*	6 + 1*
India	4	2	6
Europe	3	0	3
Central Asia	4	0	4
Asia Minor	2	0	2
Eurasia	1	0	1
Kashmir	1	0	1
Philippines	1	0	1
Madagascar	1	0	1
Eastern North America	1	0	1
Total	89	5 + 2*	94 + 2*

* Indicates similar products (e.g., rhinoceros horn) from two different species of these areas are both present in Chinese markets.

traveled with man unnoticed and have become weeds in China. Due to the climatic and ecological requirements of species from the humid tropics in southeastern Asia and the hot, dry arid lands of southwestern Asia, approximately 30 percent of the exotic plant elements and all of the animal products from those areas used in TCM are still imported.

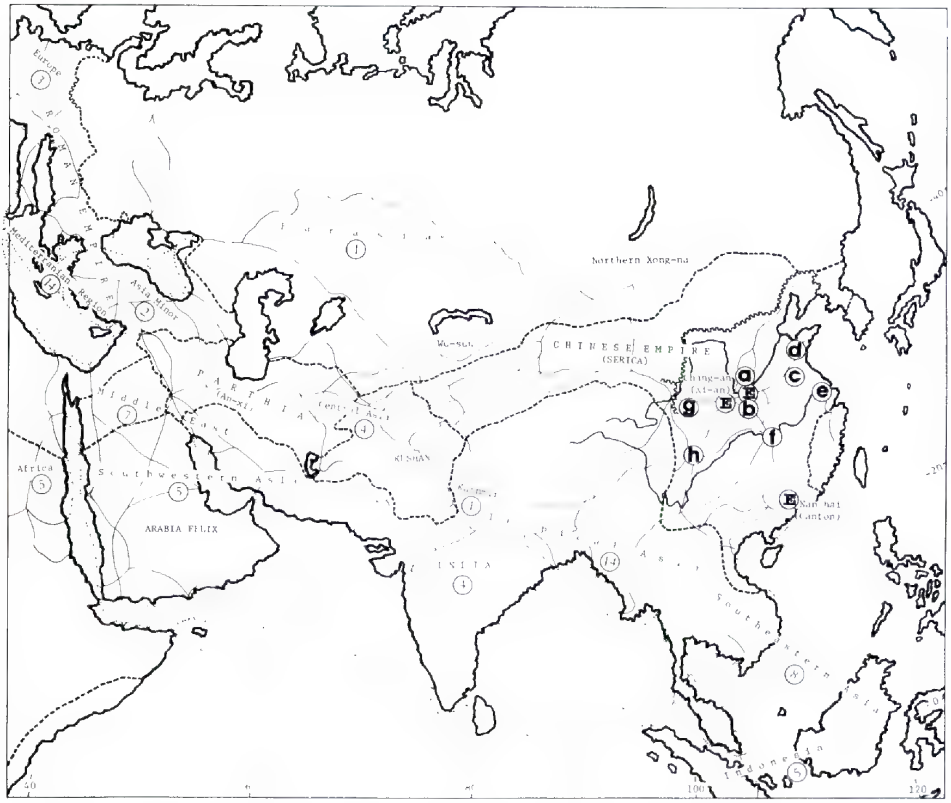
GEOGRAPHICAL ANALYSES

The geographic accounts provided here deal with the origins of the extra-Chinese elements used in TCM and the possible routes by which they were introduced. All the species are covered, whether they are cultivated, weedy, or foreign commercial products sold in Chinese markets.

SOURCE AREAS AND SPECIES

The names used for the source areas are loosely geographic, without any political significance. A summary of these areas and the number of species they have provided is given in TABLE 2.

The areas contributing most of the exotics used in TCM are tropical Asia, the Mediterranean region, and tropical America. Next in numbers of source species are southeastern Asia, the Middle East, southwestern Asia, Central Asia, Indonesia, and India. Europe has three species, Asia Minor has two, and the remaining areas have one each.



MAP 1. Asia ca. A.D. 100 showing routes of introduction of exotic elements used in TCM. Numerals denote number of species in each area. a, indicates royal residence of Emperor Yu. b–h, collecting centers of 9 tributary principalities of Emperor Yu: b, Yu-zhou; c, Xu-zhou; d, Qing-zhou; e, Yang-zhou; f, Jing-zhou; g, Yung-zhou; h, Liang-zhou. E represents three exchange centers in Chang-an (Xi-an), Guang-zhou (Canton), and Luo-yang.

ROUTES OF INTRODUCTION

The possible routes by which exotic species were introduced for cultivation or naturalization and over which exotic market products were transmitted are shown on a map of the major national and international paths of communication before and after the discovery of America at the end of the fifteenth century. In the foregoing discussion of the time of introduction of exotic elements into China, the first recorded time was in the Han Dynasty. MAP 1 shows the routes of communication within China and between nations of the East and the West. It represents a synthesis of information from Chinese and western sources.

The explanation of possible routes for the introduction of exotic elements used in TCM follows several principles. The first is that plants follow man, and ancient man traveled extensively over the earth. There are many records concerning the travels of ancient peoples. In China, during the reign of Emperor

Yu (2205–2198 B.C.), the supplies of the royal family were transported from the collecting centers of the nine tributary principalities (see MAP 1, a–h). These supply routes had become so effective that by the Tang Dynasty (A.D. 618–905) the most perishable tropical fruit, the litchi, was transported fresh from Guangzhou to Xian (Changan).

Ancient people did travel! When Confucius (B.C. 511–479) traveled with his disciples among the rulers of the feudal states, attempting to convince political leaders to accept his Doctrine of the Mean and to try his method of achieving national prosperity by starting with the well-being of the Chinese people, his contemporary, Herodotus, traveled in western Asia in Persia and many countries in the Mediterranean region, Europe, and northern Africa. Historical records from this time give no indication of direct communication between East and West. Nevertheless, the intermediaries had been successful in spreading African species such as *Sesamum orientale* and Central Asian taxa like *Cannabis sativa* to China.

The first recorded direct East-West contact that exerted obvious effects on the introduction of Chinese exotics was the famous Zhang Qian Mission to the West. However, before this Mission was possible, Emperor Wu had to make preparations by waging war to conquer rebelling chieftains and by sending gifts or negotiating marriages to appease less-resistant leaders of the ethnic peoples of the Central Asian steppes. In some of the military or diplomatic missions, thousands or even tens of thousands of people were involved. Even in Zhang's Diplomatic Mission to the Middle East, sixty-thousand people went with gifts, tributes, and weapons, as well as provisions and food for his men and animals. Plants followed man in war and peace in both directions. In Chinese history, after Zhang's mission, one of the captains responsible for safeguarding the communication route escaped with his men and settled in Armenia. He became an adviser to the Armenian king, helped him to achieve prosperity, and received high honors there. Consequently, together with the Chinese people and their lifestyle, plants were introduced to Armenia, the apricot (*Prunus armeniaca* L.) being the best-known example.

By this time in Chinese history, a great agricultural civilization had developed. Although kingdoms emerged and disappeared, palaces were built and destroyed, and wars occurred within and without, Chinese farmers continued working the land, discovering the secrets of nature, and trying to make the best use of all aspects of the environment to enable them to survive and to live better. One of the most outstanding features of Chinese agriculture was sericulture — domesticating a worm that produced silk, which could provide clothing and comfort at home. This aspect of Chinese agriculture gradually became very successful, providing splendor in courts, a medium for exchange, and a commodity for international trade.

Silk has played an important role in China's foreign relations. It has been used as a medium of exchange, as gifts for all the foreign ambassadors that came to pay homage to the emperors, and as a commodity of trade with the West. Actually, China was first known to the West as Serica, the land of silk. The routes for silk export were many, and they radiated in all directions; over them, in turn, exotics were introduced into China.

Once a route of communication was opened, the traffic continued unless stopped by some natural or manmade calamity. From the earliest record of exotics, we know that in or before the Han Dynasty at least four routes of communication were opened: land routes to the Mediterranean region and Africa, to Central Asia, and to Eurasia, Kashmir, and tropical Asia; and a sea route by which rue, dates, and henna were imported to South China by Arabs. Three centuries later, in addition to the products introduced over the ancient Central Asian trade routes, aromatic products from southeastern Asia entered China. During the Tang and Song dynasties, the volume of imports and the number of items continued to increase by both the land and sea routes. It is worthy of note that in the early days, few items were introduced from India. It was only in the Tang Dynasty that myrobalan was imported, and in the Song Dynasty that bauchee seed was recorded for the first time. During the Ming Dynasty tamarind, a species widely cultivated in India, was introduced into Yunnan. Exotics continued to be imported via many of the ancient trade routes after the discovery of the New World and the emergence of ports for international trade in the maritime provinces.

The fifteenth century was an era of maritime exploration and colonization by European countries. Soon after Christopher Columbus discovered the New World and Spain colonized tropical America, Vasco da Gama of Portugal sailed from Lisbon for Asia and returned with pepper (*Piper longum* and *P. nigrum*) from Malabar. Twelve years later Portugal captured Malacca, and three years after this the Portuguese reached China. In all the main ports of southeastern Asia the Portuguese found that important businesses were managed by Chinese residents. For over one hundred years before the arrival of Europeans, the Chinese Empire of the Ming Dynasty had a vigorous maritime enterprise in the western Pacific and Indian oceans. In 1405 the King of the Straits of Malacca submitted to China and became a protectorate of the Ming Empire. Five years later a Chinese naval force conquered King Wijayababu VI of Sri Lanka and brought him as a captive to China. When Ferdinand Magellan arrived in the Philippines in 1519, he found Chinese vessels in all the important trading ports. From the middle of the sixteenth century onward, the Philippine Islands were Spanish, annexed to Mexico. The overseas Chinese are well known for their loyalty to China; in their return trips they brought back to Fujian and Guangdong seeds and other propagules of plants they had learned to like. The red pepper and guava are good examples. At present, red pepper is cultivated in gardens throughout China, and the hot dishes of Sichuan and Hunan have won praises in metropolises worldwide. Guava is naturalized in Guangdong and Hong Kong, where people assume it is a native species.

After 1842, China was forced to open her ports for international trade. British citizens were hired by the Qing emperors and the Empress Dowager to manage the Imperial Maritime Customs. British residents in Chinese ports lived in beautiful homes decorated with exotic ornamental plants. Some of these species were first brought from the Americas into hothouses in London and were later distributed to British citizens throughout the world. Some of them—for example, *Lantana, Mimosa, Mirabilis,* and *Cleome*—arrived in China. After they were grown by the Chinese people or escaped from cultivation, they were used

for medicinal purposes in China. Meanwhile, British businessmen brought medicinal products such as senna from India and ivory from Africa into Chinese markets for profit. The United States shared the economic interests of the western powers in China. American clippers sailed between Boston and Guangzhou carrying American ginseng and other commodities—including opium—for China, and tea, cotton, silk, and porcelain were acquired in return.

PRACTICAL ASPECTS

In a span of four millennia and from places extending over all habitable continents of the earth, plant and animal products have been introduced into China, where they have been used for medicinal purposes. Why are these substances used in healthcare? Is it merely psychological and cultural, or are there certain physical and chemical bases for such practices? This is a complicated subject to be discussed in a limited space. However, a few examples can be given to illustrate the nature of the issue.

Plants Introduced for Daily Necessities

An analysis of the nature of the extra-Chinese plants and their role in Chinese culture shows that a majority of the species were introduced by people as daily necessities (for example, food and fibers) or for pleasure (e.g., fumitories, masticatories, or ornamentals). These species are still cultivated primarily for the same purpose for which they were introduced, with medicinal uses secondary. The best examples are the radish (*Raphanus sativus*), the hyacinth bean (*Lablab purpureus*), and sesame (*Sesamum orientale*).

Radish. The radish probably came with Neolithic people from the Mediterranean region as a fast-growing vegetable (the small fleshy root or just the greens). Through selection and cultivation by ingenious Chinese farmers, hundreds of varieties were selected to fit the climatic and ecological conditions of a country extending from the seashore in the east to the arid plateau in the west, so that people might have fresh or pickled radish throughout the country and at all times of the year. Radish seeds are used in Chinese medicine as a tonic for internal organs and for improving strength. In villages, after the seeds are harvested, the old dried roots are saved for making a tea to improve digestion and to cure gas pains. Phytochemists have isolated many organic acids from the radish, including coumaric, caffeic, ferulic, and gentisic acids. Radishes are very rich in calcium.

Hyacinth beans. The hyacinth bean is a common vegetable in the frozen-food section of groceries in America, where it is sold as "Italian beans." In China it is cultivated for the young fruit, which is used as a vegetable. However, the mature seed is prescribed for diabetes mellitus. It is rich in protein, calcium, phosphatide, pantothenic acid, phytin, and tyrosinase.

Sesame. Sesame is cultivated for its seeds, which are an important source of edible oil. It is prescribed for the treatment of both external and internal ailments. Sesame is rich in protein and calcium and contains arachic, linoleic, and palimitic acids, sterols, sesamin, sesamolin, sesamol, and vitamin E.

Exotics Introduced as Medicine

Approximately one-third of the exotics were imported into China for use as medicine. A few examples of the imported extracts, resins, aromatics, and animal products (aloë from Africa via Arabia, asafetida from Central Asia, gambier from India, gamboge from Thailand, and rhinoceros horn from southeastern Asia) are selected to show the reasons for their importation.

Aloë. Aloë was first introduced into South China in the form of a reddish brown extract by Arabian traders. Most of its Chinese names were direct translations from the Arabic. In the *Pharmacopoeia of Kai-bao Reign* (A.D. 973), it was recorded as a resinlike powder from Persia. When ancient Chinese consumers asked the trader the *nature* of the material, they were told "elephant bile," due to its bitter taste. For this reason it was also recorded as *xiong dan* in Chinese literature. The material is an extract obtained from the leaves of *Aloë barbadensis,* a spiny succulent perennial attaining a height of 1 m (see Figure 2). "Chinese aloë" entered China from the south and has become naturalized in many parts of Fujian. Although there is no record of the introduction of the plant to South China, we know that it has been grown, segregated and developed into special forms there. In 1817 a living aloë plant was taken from South China to London. Adrian Haworth, a specialist in succulent plants, recognized a distinctive leaf feature (spots on both surfaces) and provided the name *A. barbadensis* var. *chinensis* (Haworth, 1819). Individuals were cultivated in British gardens under this name until J. G. Baker, on the basis of a flowering plant, renamed the taxon *A. chinensis* and determined it to be closely related to *A. abyssinica* (Baker, 1877).

In Chinese medical practice aloë has been used in combination with *Pinellia* tubers (Araceae), *Atractylodes* rootstock (Compositae), and licorice for the treatment of convulsions and epilepsy in children and adults. It contains aloenin, aloin, alomicin, aloesin, barbaloin, p-coumaric acid, protein, and calcium-oxalate crystals. Recently an Aloë Association was organized in South China to promote the cultivation of aloë and the production of medicines and cosmetics from them. Among my houseplants there is an old aloë (see Figure 2a) with unspotted, grayish, lanceolate leaves, spiny along the margin. Two years ago I put it out in the yard. By the end of the summer, many suckers had arisen from beneath the surface of the soil. I transplanted the suckers and repotted the mother plant. The immature plants appeared very different from the old one in that their leaves were erect, terete, and spotted throughout. Two years have passed; these young plants all have spotted leaves, the character used by Haworth in the description of *Aloë barbadensis* var. *chinensis.* China really has no native aloë, and the feature used in identifying the Chinese aloë is unstable, changing with the age of the plants.

Asafetida. With respect to animal and plant resources for medicinal use, Central Asia is a land of poverty. In spite of geographic proximity, the only plant product imported from there into China for medicinal purposes is asafetida (*Ferula assafoetida*), known in TCM as a-wei. The crude drug is an irregular tearlike oleoresin with a powerful, foul odor and an acrid taste. The source species is a perennial herb that requires five to 18 years of vegetative

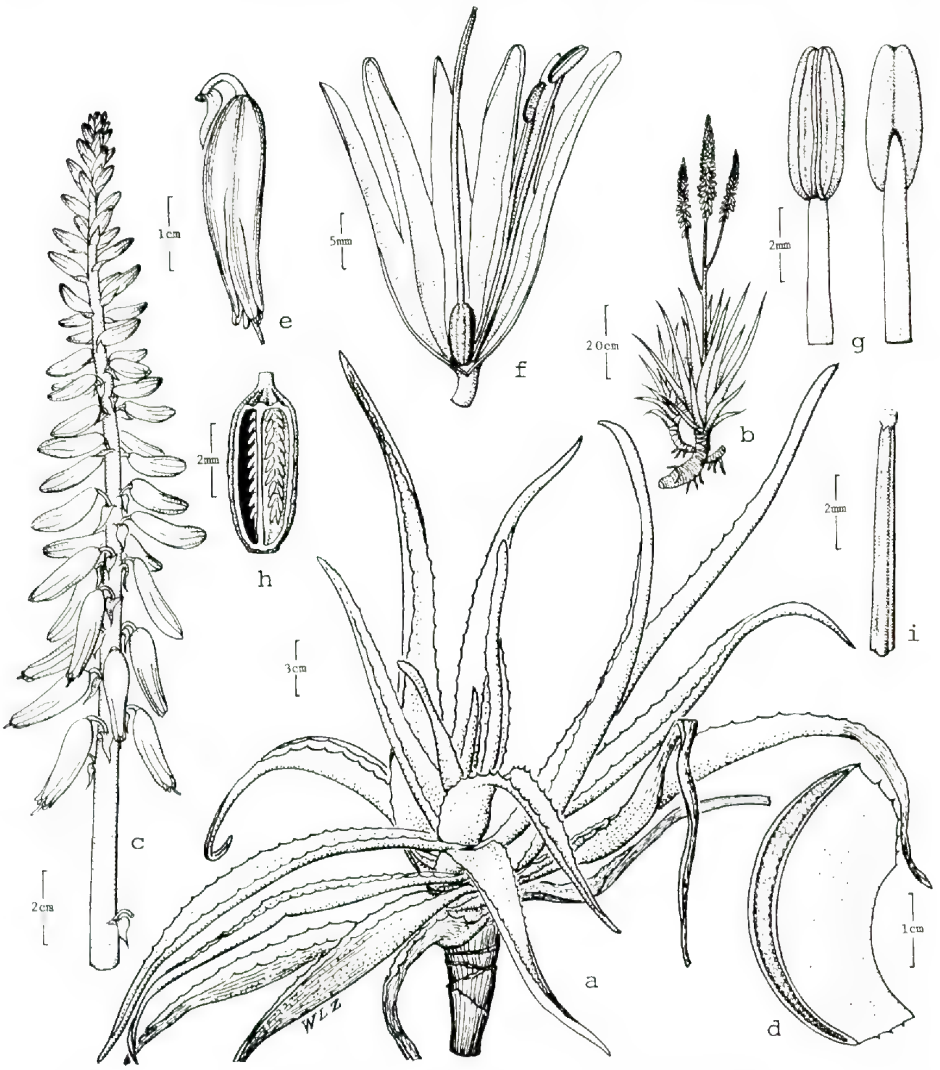


FIGURE 2. *Aloë barbadensis,* source species of commercial aloë: a, habit; b, flowering plant, showing branched scape; c, portion of flowering branch, showing position of fully open flowers; d, section of leaf, showing mucilaginous central portion; e, flower, showing outer perianth segments connate for basal half; f, flower, perianth split open and 4 stamens removed, showing ovary and free margin of inner segments; g, portions of 2 stamens, showing abaxial and adaxial views of anthers; h, vertical section of ovary; i, apical portion of trigonous style and stigma.

growth before it sends up an erect flowering stem. The people of Central Asia use the fresh leaves in food as Europeans use parsley. The straight, stout, canelike flowering stem (see FIGURE 3) can attain a height of two meters. The compound cauline leaves gradually become smaller upward, with the middle and upper ones subtending the flowering branches. The lower umbels bear staminate flowers only, while the upper ones include some perfect flowers as well. Each plant may produce hundreds of small, flat fruits; these split vertically

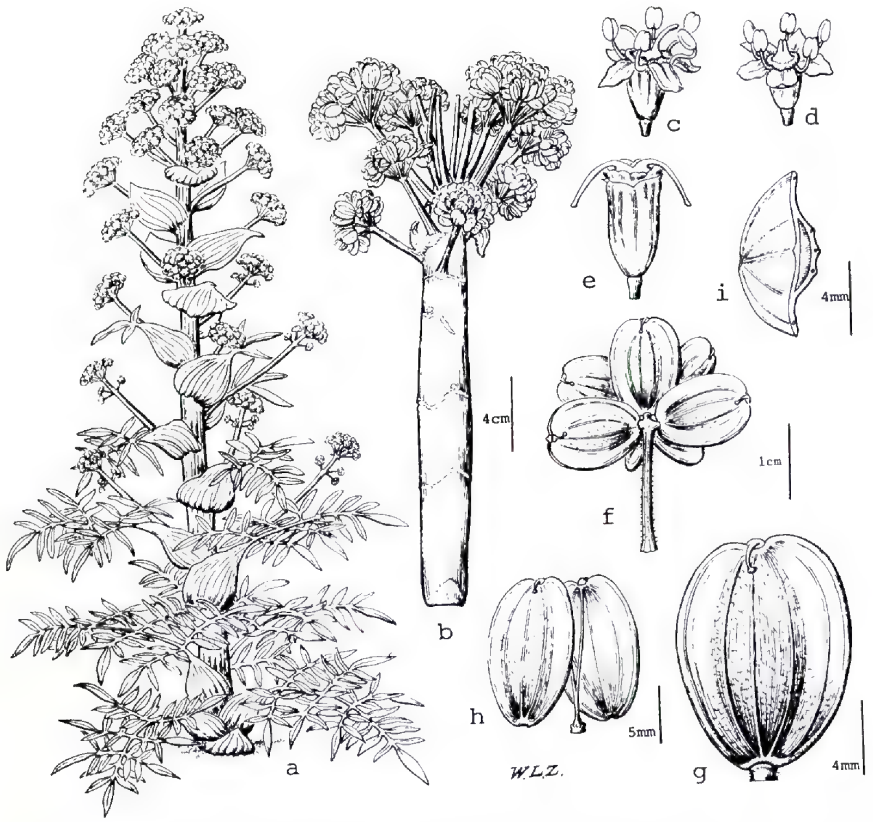


FIGURE 3. *Ferula assafoetida*: a, single erect stem bearing bipinnately compound lower leaves, laminas progressively smaller toward apex and finally constituting bracts subtending flowering branches; b, fruiting branch consisting of many compound umbels; c, perfect flower, showing elongate styles; d, staminate flower; e, young fruit; f, fruiting umbel; g, fully grown fruit; h, mature fruit after separation of mericarps, and attached at the top to the carpophore; i, a transverse section of a fruit showing the broad wings and the longitudinal canals (vittae).

into two winged mericarps, each containing one tiny seed. The mother plant dies after the seeds mature.

Asafetida is collected by removing the soil around the crown before the plant flowers, then cutting off a portion of the crown and protecting the plant from the sun. A thick, milky juice exudes from the cortex of the fleshy rootstock, collects on the surface, and hardens. After ten days the hardened mass is gathered, and another portion of the stem is cut off to let fresh juice ooze out. This process is repeated every ten days until the plant is exhausted, which usually takes about three months. The rootstock eventually dies.

Asafetida was introduced into China by Arabian traders over the sea route and first appeared in the pharmacopoeia of the Tang Dynasty (A.D. 659). A-wei was a Cantonese translation of the Arabian trade name. It is used for indigestion, lack of appetite, and gas pain. It contains volatile oils (10–71 percent), resin (40–64 percent), gum (25 percent), and ash (1.5–10 percent). Approximately

45 percent of the volatile oils is sec-butyl propenyl disulfide, which imparts the characterstic foul odor to the product. Ferulic acid and farnesiferol have also been identified. A-wei pills are available for pains of the chest and sides and lack of appetite. These are made from 7.5 g asafetida softened in vinegar into a paste, 15 g costusroot, 15 g betel nut, and 7.5 g black pepper. The powered costusroot, betel nut, and black pepper are mixed with the softened asafetida and cemented with cooked millet to make pea-sized pills. Taken with ginger tea, these are said to open up the internal physiological channels. The recipe is adapted from the well-known collection *Life Saving Recipes.* Recently, two species growing in Xin-jiang, *Ferula caspica* and *F. conocaula,* have been identified as alternative source species for a-wei.

GAMBIER. Gambier is prepared by decoction and evaporation from the heartwood of a tropical tree, *Acacia catechu* (see FIGURE 4). The plant, which may attain a height of 6–12 m, has bipinnately compound leaves, very tiny leaflets ciliate along the margin, small, yellowish flowers crowded in an elongate spike, and flat pods.

In tropical Asia gambier is chewed with betel nut. It is exported for tanning and dyeing. In China it is combined with an equal amount of the dried tuber of *Bletilla striata* (Thunb.) Reichb. f. (bai-ji), pulverized, and applied to sores in the mouth and boils. Gambier is an astringent containing catechutannic acid, catechin, epicatechin, phlobatannin, fisetin, quercetin, quercetagetin, protocatechuic tannins, and pyrogallic tannins. The tree has been introduced into Yunnan Province for commercial production.

GAMBOGE. Gamboge is a resin prepared from *Garcinia morella,* a tropical tree 18 m tall with opposite leaves, small, yellow, unisexual flowers, and juicy, round fruits (see FIGURE 5). The material is prepared by making incisions in the bark. A viscid yellow juice oozes out and dries on exposure to air.

The resin is collected in hollow bamboo sections, where it hardens into cylinders. It is soluble in water, alcohol, and oil and is much used by artists. It is fatally poisonous if taken internally. At present, it is only produced on a few small islands in southeastern Thailand and is taken to Singapore for distribution. In China it is an important external medication for cutaneous diseases, especially carbuncles, abscesses, ulcers, scabby head, and cancerous tumors. From the material, phytochemists have isolated a-guttiferin, b-guttiferin, morellic acid, isomorellic acid, morellin, isomorellin, dihydroisomorellin, ethoxydihydroisomorellin, morelloflavone, and neomorellin.

RHINOCEROS HORN. Whole horns have been brought into China from Thailand, Java, Sumatra, India, and adjacent tropical areas for medical use since prehistoric times. More recently, horns have also been imported from Africa for the same purpose. Rhinoceros horn was recorded in the first Chinese herbal, *Herbal Classics of the Divine Plowman,* and it is still in common usage. In TCM rhinoceros horn is used in the form of slices or powder and serves as a cooling and detoxifying agent, or as an ingredient in the preparation of emergency remedies for quick relief of heatstroke, high fever with delirium, or convulsions in children; there are many ancient formulas for it. After World War II medical scientists began to investigate its chemical composition and to study its pharmacological effects with animal assays. It has been found that

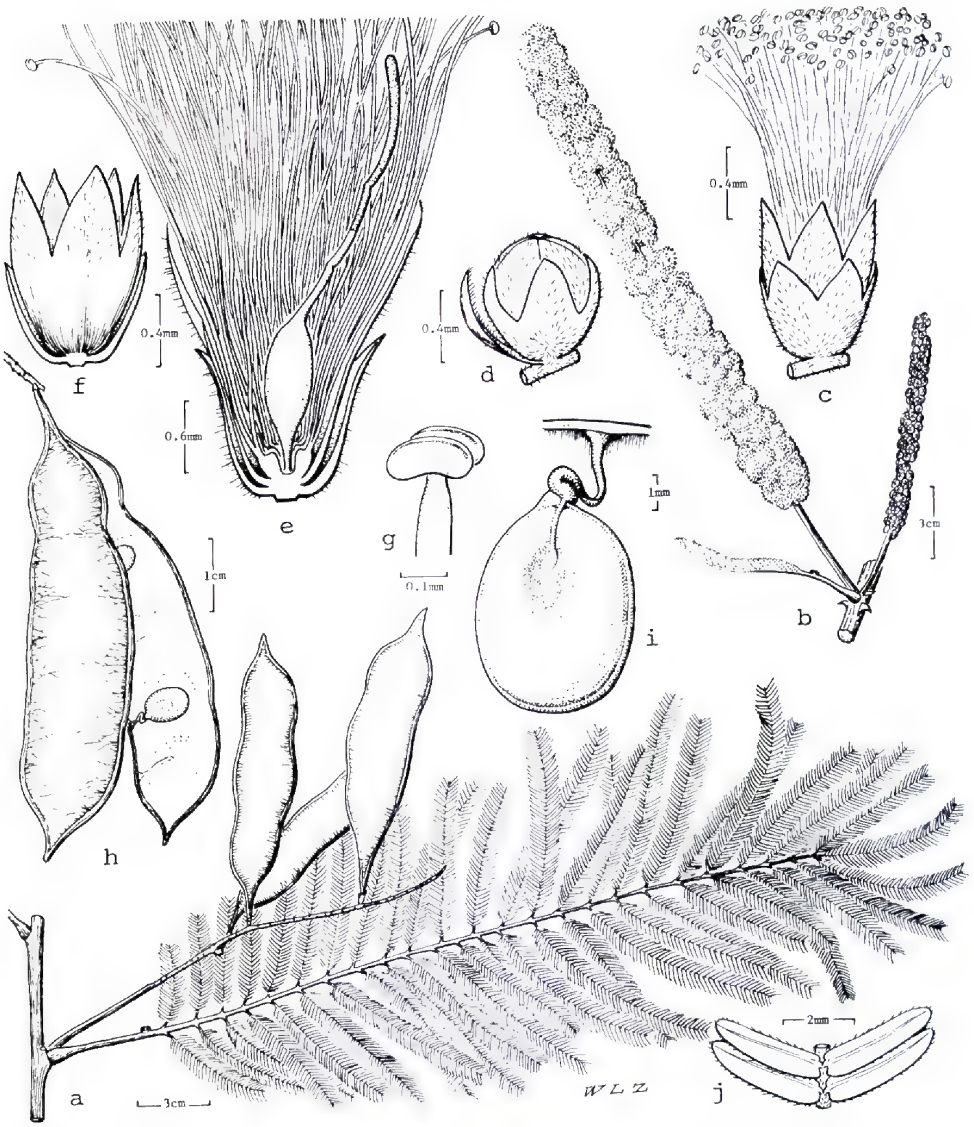


FIGURE 4. *Acacia catechu*: a, a fruiting branch showing 3 fruits and 1 even-bipinnately compound leaf with gland on adaxial side at apex of petiole; b, portion of growing young shoot, showing unfolding leaf with petiolar gland and 2 axillary spikes, 1 with flowers and 1 with buds; c, a sessile flower, showing small calyx and corolla and numerous stamens; d, flower bud subtended by linear bract; e, vertical section of flower, showing calyx tube, corolla, very short and stout staminal tube, threadlike filaments, and pistil consisting of ovary and clavate style; f, flower with portion of calyx, stamens, and pistil removed to show campanulate corolla; g, apical portion of stamen, showing attachment of anther; h, mature dehiscent fruit, showing 2 seeds; i, portion of fruit, showing seed with sigmoid funiculus attached to adaxial suture of pericarp; j, pair of leaflets, showing ciliate margin.

rhinoceros horn is very rich in protein (keratin), particularly in cystine, histidine, lysine, and arginine. It also contains peptides, guanidine derivatives, cholesterol, and asparagic acid. Water extracts of rhinoceros horn excite the muscles of isolated toad hearts and of *in situ* rabbit hearts. It strengthens

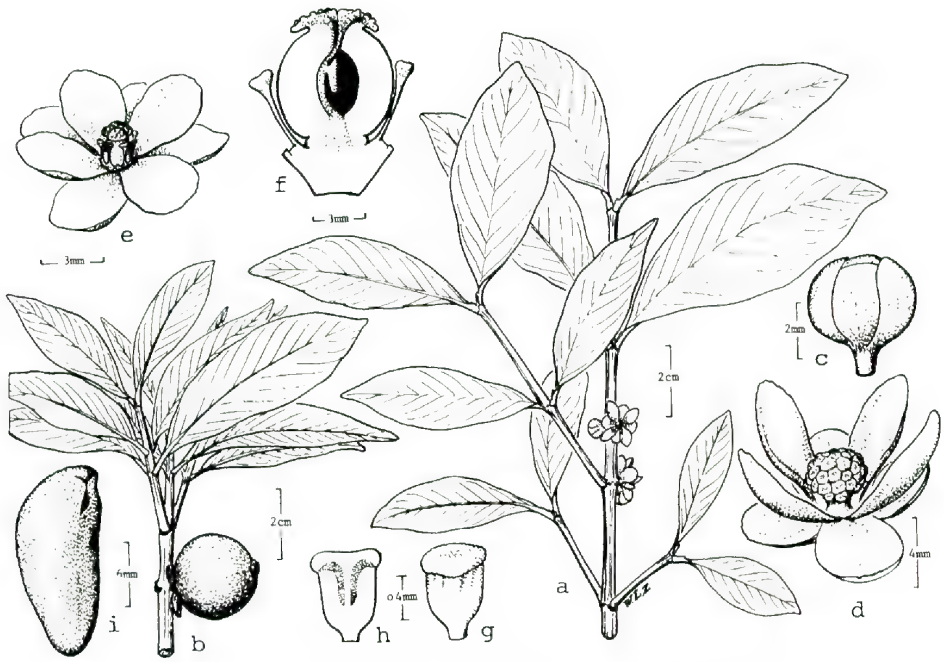


FIGURE 5. *Garcinia morella*: a, flowering branch, showing opposite leaves and staminate flowers; b, a fruiting branch, showing a fruit with persistent calyx; c, mature flower bud; d, staminate flower, showing 4 sepals, 4 petals, numerous stamens crowded at end of stout androphore; e, pistillate flower, showing staminodes and ovary; f, longitudinal section of very young fruit, showing position of ovule; g, stamen showing very short filament and orbicular apex of connective; h, vertical section of stamen, showing thecae and the thin position for dehiscing; i, lateral view of dried immature seed with elevated raphe and germination.

heartbeats and increases blood flow. Intravenous injections reduce experimentally induced fever. In the hind legs of toads it causes temporary short contractions followed by relaxation; it also relaxes the smooth muscles isolated from the intestine and uterus of rabbits.

EMERGENCY REMEDIES

Hospitals and ambulance services were unknown in China before 1910 and are rarely available to the general public today. In emergencies, such as heatstroke, convulsions in children, delerium and high fever, or loss of consciousness, the Chinese people rely primarily on rescue remedies. These preparations are composite formulas designed through the accumulation of knowledge and experience. These remedies are circulated in several forms—for example, pills (wan), powders (san), and red-coated elixir (dan)—that are available without a prescription. A random selection of ten of these emergency remedies from *A Handbook of Chinese Pharmaceuticals in Traditional Medicine* (Shong Yao Zhi Ji Shou Ce; Anonymous, 1974), reveals that each contains some imported material in amounts varying between 0.5 and 78 percent by weight. The number

of ingredients in these rescue remedies varies from six in a cardiovascular pill (guan-xin su-he wan) to 50 in a blood-flow activator (shen-xue huo-luo wan). The amount of herbal material taken is very small, with 90 percent of the dosages being less than 1 g. Translations of two samples are presented below to show the nature of the remedies and the importance of exotic elements in their preparation. In the recipes, only the ingredients now imported from abroad are marked with asterisks. Products from the cultivated extra-Chinese elements, such as fennel seed from *Foeniculum vulgare* and menthol from *Mentha haplocalyx,* are not marked.

PEOPLE'S ELIXIR (ren-dan): *Alpinia katsumadai* Hayata,* Katsumada's galanga, 31 g; *Amomum villosum* Lour., grain-of-paradise, 31 g; *Areca catechu* L.,* betel nut, 31 g; *Canarium album* (Lour.) Raeusch., Chinese olive, 31 g; *Carthamus tinctorius* L., safflower, 15.5 g; *Cinnamomum loureiroi* Nees, Saigon cinnamon, 31 g; *Citrus reticulata* Blanco, Mandarin orange peel, 31 g; *Dryobalanops aromatica* Gaertner,* Borneo camphor 7 g; *Foeniculum vulgare* Miller, fennel seed, 31 g; *Glycyrrhiza uralensis* Fischer, licorice, 248 g; *Mentha haplocalyx* Briq. (or *M. arvensis* L.), menthol, 28 g; *Poria cocos* (Schw.) Wolf, Chinaroot, 31 g; *Saussurea lappa* (Dcne.) C. B. Clarke,* costusroot, 46.5 g; *Syzygium aromaticum* (L.) Merr. & Perry,* cloves, 15.5 g; *Moschus moschiferus* L., musk, 3.1 g. The finished product is packed in tiny glass bottles as small red pills coated with cinnabar, each weighing 0.03 g. The dosage varies from between three and 20 pills, depending on the situation. In this formula, 20.5 percent of the ingredients by weight are imported.

ROYAL STORAX PILL (su-he-xiang): *Aquilaria agallocha* Roxb.,* aloeswood, 31 g; *Boswellia carteri* Birdw.,* frankincense, 31 g; *Cyperus rotundus* L., nut grass, 31 g; *Dryobalanops aromatica* Gaertner,* Borneo camphor, 15 g; *Liquidambar orientalis* Miller,* storax, 15 g; *Piper longum* L.,* long pepper, 31 g; *Santalum album* L.,* sandalwood, 31 g; *Saussurea lappa* (Dcne.) C. B. Clarke,* costusroot, 31 g; *Styrax benzoin* Dryand. (or *S. tonkinensis* (Pierre) Craib),* benzoin, 31 g; *Syzygium aromaticum* (L.) Merr. & Perry,* cloves, 31 g; *Terminalia chebula* Retz,* myrobalan, 31 g; *Rhinoceros bicornis* L. (or *R. sumatrensis* Cuvier),* rhinoceros horn, 31 g; *Moschus moschiferus* L., musk, 23 g; and cinnabar, 31 g. This formula was first designed in the royal palace during the Song Dynasty and is still used. It calls for 14 ingredients, of which 11 (78 percent by weight) are exotics. The finished product consists of pills weighing ca. 3 g including the cementing material. Each dose contains ca. 0.16 g of herbal material.

CRITERIA FOR DETERMINING EXOTICS

In the foregoing list of exotics in Chinese materia medica (TABLE 1), items (e.g., *Abutilon theophrasti* and *Cannabis sativa*) are included that were formerly

recorded, on the basis of assumption, as native to China (Spencer, 1984; Wang & Guo, 1980). Various other native Chinese plants (e.g., *Juglans regia*) that used to be regarded as introduced on the basis of hearsay are absent. After extensive field observations of the ecological conditions in China, investigations of ethnobotanical practices within the country, and intensive phytogeographical, systematic, and cytotaxonomic studies made in the herbarium and the library of the Harvard University Herbaria and the Chinese Library of the Harvard Yenching Institute, I used five criteria for determining which elements used in TCM are exotics. 1) Ecologically, the species is not adapted to grow in the natural flora or fauna of China and is thus dependent on man for survival. 2) Morphologically, it is a distinct taxon without closely related species in China. 3) Biogeographically, the center of species concentration is in a region far from China. 4) Cytologically, its chromosome complement is of high ploidy. The diploid progenitors are in distant phytogeographical areas. 5) Historically, plants and animals have moved with people and are changed by them; the routes of such movement are often traceable.

Application of these criteria proves positively that *Abutilon theophrasti* and *Cannabis sativa* are exotic elements in the flora of China and establishes that *Jasminum sambac* is not Arabic and *Juglans regia* is not Persian. The latter two species are indigenous to China, selected and developed by the ancient ethnic groups dwelling in areas where the wild species grew.

ABUTILON

In northern China *Abutilon* constitutes a minor fiber crop or—particularly in neglected disturbed areas of large cities such as Beijing, Nanjing, and Wuhan—is a weed. It was repeatedly introduced from China into the United States as a potential source of fiber for cordage. It has been called Indian mallow, stampweed, buttonweed, and Chinese velvetleaf and has become a troublesome weed in fields of corn, cotton, and soybeans. Spencer (1984) has estimated that the annual economic loss due to velvetleaf is approximately $343 million. In response to the request of American weed scientists, in 1984 I searched for the natural enemies of *Abutilon* in China, hoping to find some special animal or plant pathogens that I could bring back for the biological control of velvetleaf in the United States. From Hong Kong, I entered China and traveled all the way to Guangzhou, Lanzhou, Qinghai, Inner Mongolia, Datong in Shanxi, Beijing, Wuhan, Nanjing, and many areas in Jiangsu (including where *Abutilon* was formerly cultivated on my grandmother's farm) but failed to find any specific natural enemy. I studied the ecological conditions of the plants, took photographs, and collected voucher specimens. Subsequently, I concluded that *Abutilon* is not native to China. Occuring only in association with man, it is an isolated tetraploid with the related diploid progenitors growing in southwestern Asia. Apparently, what is known as the Chinese velvetleaf (*A. theophrasti*) was unintentionally introduced into China, having attached itself to man or his animals; it later became naturalized and was gradually domesticated and improved by Chinese farmers to furnish the bast fibers used in cordage

and for making sandals. The medicinal use of the seed was first recorded in a seventh-century herbal. It is worthy of note that in the vicinity of Hong Kong and Guangzhou, the tetraploid perennial *A. indica* (L.) Sw. grows as a weed. Apparently the species of *Abutilon* in China are all adventives.

Cannabis or Hemp

The worldwide distribution of *Cannabis sativa* is mostly man related. Humans have captured and capitalized on the genetic variability and ecological plasticity of the species and have used it to meet their special needs. In India and now in Latin America, it has become a cash crop. Young fruits and leaves are harvested and used as a narcotic drug. Large quantities of the drug are sold in the United States as marijuana, the use of which has caused serious social problems. In China it is extensively cultivated as a minor crop for the useful bast fiber, which is stronger but less plentifully yielded than that of *Abutilon.* The medicinal use of its by-products (seeds, roots, bark, leaves, and young fruits) has not been important to Chinese farmers, at least not before the 1930's when I lived among them during the harvest season.

The origin and the systematics of the species of *Cannabis* have puzzled botanists throughout the history of botanical science. In China hemp appears in the earliest plant records as *ma,* which has become a generic term for different types of bast fibers and the names of their source species—for example, *huang-ma* for jute (*Corchorus capsularis* L.), *qing-ma* for velvetleaf (*Abutilon theophrasti*), and *zhou-ma* for ramie or China grass (*Boehmeria nivea* (L.) Gaud.). Archaeological evidence shows that *Cannabis* was associated with Neolithic dwellers in Gansu, the cradle of Chinese civilization (Wang & Guo, 1980). In this case, antiquity does not prove that *Cannabis* is indigenous to China, for the seeds were kept in an earthenware jar. *Cannabis* is an exotic element in the flora of China because its existence in the country is completely dependent on man. It is noteworthy that the young fruit, the most potent organ of the plant used in marijuana, was recorded in ancient Chinese classics, *Er-ya,* as *ma-fen* (ma grave) or *ma-lan* (blue ma or ma cradle). As a medicine, 0.6 g of *ma-fen* is given to patients with the warning that the material is poisonous, and when taken in excess it ruins a person, making him violent and crazy. The active principle is a resinous substance containing tetrahydrocannabinol (THC), which gradually disappears as the fruit matures. The Chinese people use ripe seeds as feed for pigeons fattened to be served in special restaurants.

Jasmine

The origin of the source species of *mo-li-hua,* used in the Chinese tea industry to produce the delicate flavor of jasmine tea, has been both erroneously recorded in botanical literature and misinterpreted in Chinese references. In classic botanical works, Linnaeus (1753) and Aiton (1789) cited two records based on plants introduced from Arabia and cultivated in European gardens under the common name "sambac." In 1753 Linnaeus proposed *Nyctanthes sambac* L.,

which Aiton transferred to *Jasminum* L. in 1789 to validate the currently used scientific name, *J. sambac* (L.) Aiton. Aiton also added the English name Arabian jasmine. In ancient Chinese writings, *mo-li-hua* first appeared in *Nan-fang cao mu zhong* (*A Description of Plants from the South,* A.D. 306), by Ji Han. Ji was from a famous educated family of the time. Through family connections he was appointed Awestricken General and Prefect of Xiang-yang. Xiang-yang (long. 122°8′ E, lat. 32° N) was an important communications post where diplomatic missions and merchants from southern China stopped to change means of transportation from boats to horses to continue along their journeys to the capital. At that time valuable tropical natural products such as ivory, rhinoceros horn, spices, and perfumes were sent as tributes to the emperor, kings, dukes, and local officers, or as material for exchange gifts. In Ji Han's office, a record of these products was made under the title *Nan-fang cao mu zhong.* When Li was assassinated in 306, the list contained about 80 items, each with a name and with the information supplied by the bearer. The second item on the list covers two species of *Jasminum.* The information given provided several facts. At the beginning of the fourth century, two kinds of white-flowered jasmine were transplanted from the tropics to the warm-temperate city of Xiang-yang in northern Hubei Province. Both types produced very fragrant flowers, for which the species had been domesticated in southern China (where Guangzhou was the major city). The species were native to the land west of Guangzhou—an area occupied by the Hu people, who had not adopted the Chinese culture. One species was called *mo-li-hua*; the other, *ye-xi-ming,* apparently a translation of the Persian-Arabic word "yasmin" ("jasmine" in English). The latter species has been identified as *J. officinale* L., which has compound leaves and is rarely cultivated in China.

Based on the above Latin and English names and the ancient Chinese records, early Chinese botanists began to draw the conclusion that *mo-li-hua* was native to the area between India and Arabia. Chen (1937, p. 1031) further explained, "It seems to have been introduced from southern Asia to China, first planted in South China, and now cultivated throughout the country for ornamental purposes. In Fuzhou, it is planted extensively, for there it is used to scent tea. The annual production reaches 2,000,000 catties." Actually, the areas in the vicinities of Guangzhou and Kunming both have large acreages planted with the crop.

Like other botanists of my generation, I used to believe that the *mo-li-hua* in Chinese gardens was introduced from Arabia. Then I saw the wild type of *Jasminum sambac* in Yunnan and studied the species in the natural flora of China. On 30 October, 1980, I was stranded in Si-mao after a lecture tour to the Tropical Botanical Garden, Academia Sinica, in Xi-shuong-ban-na, situated in the area of the Chinese Tai minority on the Yunnan-Thailand border. Since the small plane could not take off, I spent the extra time studying the plants in the gardens and in a nursery. Among the numerous pots of *mo-li-hua,* I saw some plants sending out one or two elongate vinelike shoots, which the nurseryman had trimmed off to produce a shrublike appearance. Suddenly I realized that I was looking at the prototype of the *mo-li-hua* that I had seen

throughout China as shrubs in pots and in gardens. Actually, I was standing on the land where early cultivators began to domesticate *J. sambac,* transforming it from its natural clambering habit to a shrubby one.

To check the validity of this insight, I examined herbarium specimens of species of the genus *Jasminum* on a worldwide basis and studied the morphological characters and distributional patterns of the Chinese species in particular. Species of *Jasminum* have a pantropic distribution. The Chinese species can be divided into two major groups: the temperate deciduous ones, such as *yin-chun* (*J. nudiflorum* Lindley) and *tan-chun* (*J. floridum* Bunge), with shrub-like habits and yellow flowers that open early in the spring before the leaves, and the tropical evergreen ones, such as *su-xin* (*J. sinense* Hemsley), *gia-su-xin* (*J. amplexicaule* Buch.-Ham.), and *su-xin-hua* (*J. officinale* L. var. *grandiflorum* (L.) Kobuski), with vinelike habits and white fragrant flowers. Some of the species have simple leaves, while others have compound ones. *Mo-li-hua* is an evergreen plant with simple leaves and fragrant white flowers that often turn purplish pink with age. On plotting the distributions of the wild simple-leaved Chinese species of *Jasminum,* I was indeed surprised to find that six of them all closely related to *J. sambac* grow in an area within a 100 km radius of Si-mao (101°02′ E, 22°24′ N). These little-known species (*J. anastomasans* Wall., *J. coarctulum* Roxb., *J. coffeinum* Hand.-Mazz., *J. dunicolum* W. W. Sm., *J. nintooides* Rehder, and *J. sequinii* Léveillé) are not yet known in cultivation. This area where the morphological diversity and species concentration of *Jasminum* occurs, called Hu in the time of Ji Han, has been termed a "favored area for evolution" by one modern biogeographer and Cathaysia by Takhtajan (Hu, 1971, p. 222). It is the homeland of *mo-li-hua.*

Nine species of *Jasminum,* including *J. sambac,* are used in traditional Chinese medicine in the form of roots, stems, and leafy shoots. Apparently *J. sambac* was domesticated in Cathaysia and gradually spread by man to Arabia, from where it was introduced to Europe. All former records that ascribed its origin to Arabia were made on assumptions, and they are botanically unrealistic: *J. sambac* and closely related species grow in the humid tropics; the arid Arabian climate does not support such plants except in gardens.

Walnut

The origin of *Juglans regia* L. has puzzled early researchers interested in Chinese economic botany and the cultural exchange between East and West. Unfortunately, at the time when Laufer (1919) conducted his research into the ancient literature dealing with walnuts, the biology of *Juglans* and the ethnobotany of the ancient people who first cultivated, selected, and improved the wild progenitor into a form like *J. regia* (which has thin-shelled nuts with edible kernels) were yet unknown. Consequently, his conclusion that the English walnut has a Persian origin contradicts modern scientific findings. Moreover, under the influence of ancient Chinese and more recent foreign scholars, early botanists in China also considered *J. regia* to have been introduced. For example, a widely circulated reference (Chen, 1937, p. 136) stated, "According to tra-

dition, the species is a native of Arabia, was introduced into China in the Han Dynasty, and is extensively cultivated in central and northern China today." The concept that the edible walnut is not Chinese should be rectified.

Current botanical data indicate that the walnut family (Juglandaceae) is old, having originated in the Northern Hemisphere. The present-day center of diversity is eastern Asia (Manchester, 1988), particularly China, where living species of *Platycarya* Sieb. & Zucc., *Engelhardtia* Leschen. ex Bl., *Pterocarya* Kunth, *Cyclocarya* Iljinskaja, *Carya* Nutt., and *Juglans* L. coexist. In Europe there are no native species of these genera, and in America only species of *Carya* and *Juglans* are indigenous. (Actually, these two genera have wider geographic distribution and more ecological amplitude in America than in China.) The natural species of *Juglans* are all monoecious, with small, green, unisexual flowers; the staminate ones are in pendulous catkins on second year growth, the carpellate ones in upright spikes terminating current year's growth. Additionally, all have lamellate pith in the young branchlets; alternate, pinnately compound, estipulate leaves; drupelike fruits, each developed from an inferior ovary, and nuts with thick shells that are very hard to break. The species with large, thin-shelled, relatively easy-to-crack nuts and tasty kernels, like *J. regia,* are of anthropogenic origin, having been selected through cultivation and/or hybridization. Botanical literature of the last two centuries has recorded many such species and horticultural forms (see Rehder, 1940, 1949). *Juglans* × *intermedia* Carr. was developed through hybridization between an American species (*J. nigra* L.) and an Asian one (*J. regia*); the thin-shelled horticultural forms *Juglans* 'Paradox' and *Juglans* 'Royal' were selected in the U. S. A. from hybrids of *Juglans hindsii* (Jepson) Jepson and *J. regia*; and *Juglans* 'James River Hybrid' from *Juglans nigra* × *J. regia.*

Ancient Chinese literature and recent ethnobotanical findings together confirm the fact that *Juglans regia* was cultivated from native wild species in China at the beginning of the Christian era. The earliest Chinese records concern the cultivation of walnuts in the capital (now called Nanjing) of the Kingdom of Wu (A.D. 222–277) and the quality of the kernel in the Eastern Jin Dynasty (ca. A.D. 326). In the royal garden called Hua-lin-yuan 84 walnut trees were in cultivation. Eastern Jin (A.D. 317–419) conquered Western Jin and used Nanjing as the capital. Fifty years later, Su Jun tried to overthrow the Jin government. The women of some rich families escaped the rebellion by going from Nanjing to Lin An Shan for safety. It was recorded that a messenger was sent to bring supplies from the capital to Lady Liu with a letter explaining the special fruits included. Regarding the walnut, the letter stated that it was originally grown in the farther land of Xi-qiang, that the outer shell was hard but the inner kernel sweet, and that it was sent as a special tribute because it was easy to carry (Laufer, 1919). The ethnobotanical significance of the above references has never been grasped by subsequent scholars (Chinese or foreign) who wrote about the edible walnut in China because they were uninformed concerning the land where the cultivated and wild species of walnut grow, or about the life, language, and culture of the people there, until China became involved in World War II.

The Sino-Japanese War began in 1937 and ended in 1945. During this period I taught in the Department of Biology, West China Union University, Chengdu. During summer vacations I hired some native hunters or medicine gatherers to help me with field work and with the study of vegetation and ethnobotany. We collected specimens of different species of *Juglans,* which they called *he-tao* (the cultivated trees in the villages) or *shan-he-tao* (the wild trees on the hillsides). In the summer of 1941, C. C. Liu (China's leading herpetologist), his associates, my assistant, and I followed a tributary of the Min River from Li-fan up the Mong-dong Valley. Opposite this valley in the mountains south of Li-fan lived the Qiang ethnic group. These people cultivated barley and corn, depended on wild onions and fern fiddleheads for vegetables, and kept dried, wild persimmons and walnuts in their houses. I was given some walnuts and shown how to crack them by placing two nuts in one hand and giving a quick squeeze. I was very surprised to know that walnuts could have such thin shells. Those that I had seen elsewhere in China had hard, thick shells and were rather rare; they were broken by a stone or a hammer. The ethnic people living in the mountain valleys of the Qiong-lai Range (Chung-lai on Map in Hu, 1956) had early selected and developed walnuts, and they continued to improve the quality to the state I had seen.

I ascended the Qiong-lai Range from different directions and reached several peaks covered by snow in August. At the level where broad-leaved deciduous forests fluorished, there were wild Chinese walnuts (*Juglans cathayensis* Sarg.) growing on the hillsides and cultivated trees of *J. regia* in the villages. In the Mong-dong Valley, the people were very proud of their special thin-shelled nuts.

The Qiong-lai Range and the adjacent land mass to the north and west were occupied by the ancestors of the Xi-qiang and by the Rong or Gia-rong. In the history of China, the name of this area has been changed many times. During the Three Kingdoms Epoch and the Eastern Jin Dynasty (A.D. 222–419) when *Juglans regia* was first mentioned in Chinese literature, the region was called "The Further-Land of the Western Qiang" by scholars. When the famous European explorers A. David and E. H. Wilson collected animal and botanical specimens there, they used "Eastern Tibet" on their labels and in their publications. When I collected in the area between 1938 and 1942, the western portion was administered by the Sikang provincial government, and the eastern portion was Sichuan (Szechuan), as printed on my field labels. On today's map of China, the entire region is in Sichuan. Early historians and sinologists misinterpreted the ancient records about Xi-qiang because they used a map of the twentieth century with the western Chinese boundary on the Pamir Mountains and took the phrase "farther land of Xi-qiang" to mean Persia. They thus shifted the origin of the walnut from western China to Persia. A botanist from Iraq, I. A. Al-Shehbaz, told me that all the walnuts in Iraq and Iran are cultivated. There is no wild species of *Juglans* in the Middle East.

The dispersal of *Juglans regia* was also through man's activities. Before 1950 the agriculture of the Qiang and Yong ethnic minorities in western Sichuan was for self-sustenance, as it was for 95 percent of all Chinese farmers. One or

a few walnut trees may have been planted near the family house to provide nuts for family use, not for sale. They were for festivities, or to be used as a rich source of energy, especially for the men on their hunting trips or during religious pilgrimages. On such trips away from home, the rations were *zhan-ba* (roasted barley meal) and walnuts. In a wayside rest station the traveler just mixed the *zhan-ba* with hot tea and butter provided by the host, supplemented by a few nuts to make a meal. Often the walnut was given in exchange for favor or for gifts.

In ancient times the Qiang people were politically and militarily involved with the people using the Chinese language and writings to their east, and the Rong minorities were religiously associated with the people on the Tibetan plateau to the west. It was evidently through such activities that walnuts were carried eastward to the people in the plains of the Yellow and Yangtze rivers, and westward into Tibet, thence to northwestern India and Persia. The common Sanskrit terms for walnut, *akhota, aksota,* and *aksosa,* seem to confirm the movement of the Chinese *he-tao* to India via Tibet.

Generally, when a cultural trait passes between two peoples living in adjacent areas, it goes unrecorded, and the people receiving it take it as a matter of fact. This was exactly the case with walnuts in the lower Yangtze provinces. Apparently, ancient scholars like Ji Han of the fourth century were familiar with walnuts. In his *A Description of Plants from the South,* when he described nuts brought to Xiang-yang by special envoy, he compared them with the taste of walnuts. For example, in recording coconut from southern China, he stated that the white meat tastes like walnut, but it has a richer flavor.

CONCLUSIONS AND DISCUSSION

Having worked with plants for over sixty years, I am habitually inclined to treat a historical problem as I do a living organism: I investigate its development, structure, interaction within a community, and reaction to time, space, and human activities. I believe that scientific methods are applicable to the study of history as well as to work with biological objects. Guided by this, I started researching the introduction of exotic elements used in TCM.

Some extra-Chinese elements were introduced into China a very long time ago. Hemp, for example, entered China with Neolithic man, according to recent archaeological evidence. There has been a continuous growth in the number of plant and animal products introduced. Meanwhile, there has been a gradual change in the nature of the importations: daily necessities such as food and fiber gave way to aromatics and spices used in the preparation of emergency remedies in the Song Dynasty, and then to substances for comfort and enjoyment of life in the Ming and Qing dynasties. The importation of 99 percent of the items can be traced in ancient records. However, when a species is used only in folk medicine, shared by people living in adjacent areas, and spread through intermediaries, the time of its introduction into China may never be known. The creat of India (*Andrographis paniculata*) in South China is a good example.

The geographic analysis shows that tropical Asia, the Mediterranean region, tropical America, and southeastern Asia have been the primary contributors of the exotic elements used in TCM. Over 56 percent of the 94 items listed came from these four areas. Most of the species were introduced intentionally, although a few plants—including the velvetleaf (*Abutilon theophrasti*)—arrived in China as adventives following the movement of man.

Since China is rich in natural resources, why are animal and plant products imported into the country for healthcare purposes? First, it should be understood that adventure is in the nature of mankind, and plants and animals move with man. A majority of the extra-Chinese plant species was first introduced into China as daily necessities such as food and fiber for the ancient travelers. Today these species are still cultivated for the same purposes. Ingenious and inventive people who tried to use the agricultural by-products effectively discovered their medicinal uses long after their introduction into China. Radish, hyacinth bean, black sesame, and cannabis seed are good examples.

Second, the geographic position and the general climatic conditions of China limit the production of certain source species that require humid tropical or warm xerophytic conditions. Certain products from the tropics are needed for soothing the unbearable pain of abscesses, ulcers, and carbuncles, and for curing tenacious cutaneous diseases such as scabby head. Gambier from India and gamboge from Thailand are imported via Singapore for these purposes. Other products are needed in the preparation of rescue remedies used in such emergencies as heatstroke, epilepsy, convulsions in children, loss of consciousness, and delirium. Frankincense, borneol, cloves, and rhinoceros horns are imported primarily for such preparations. In the popular and nationally available people's elixir, 20.5 percent of the weight of the 15 ingredients is of extra-Chinese origin. In the more expensive royal storax pill, 78 percent of the total weight of the 14 ingredients consists of imported material. Recently, Chinese pharmaceutical manufacturers have tried to use synthetic materials and/or local products to substitute for imported elements obtained from endangered species—for example, using horns of the buffalo to replace those of the rhinoceros in prescriptions. However, these efforts have not stopped the flow of exotic natural products into the country for use in TCM.

In researching the origin of extra-Chinese elements used in TCM, I have encountered numerous incorrect and untrue statements both in the botanical literature and in ancient Chinese documents. Reports of *Abutilon* and *Cannabis* as indigenous to China, of *Jasminum sambac* as a native to Arabia, and of *Juglans regia* having a Persian origin are incorrect. After months of research, I have been able to rectify these erroneous concepts; for example, *Abutilon* and *Cannabis* have been added to the list of introduced species, and jasmine and walnut have been removed from my original list of exotics used in TCM.

ACKNOWLEDGMENTS

My special thanks are due to Thomas C. Hu and Luke L. Wang for their unfailing assistance in the preparation of the manuscript, and to Beverly Huck-

ins and David E. Boufford for reading it and offering many helpful suggestions. I am deeply indebted to the staff of the Harvard University Herbaria and the Chinese Library of the Harvard Yenching Institute, Harvard University. Without the unique herbarium collections and library facilities, it would have been impossible for me to carry out this research. My interest in Chinese medicinal plants was rekindled by the enthusiasm of my colleagues on the Faculty of Science, the Chinese University of Hong Kong, and particularly by the encouragement and support of H. M. Chang, Y. C. Kong, and P. P. H. But.

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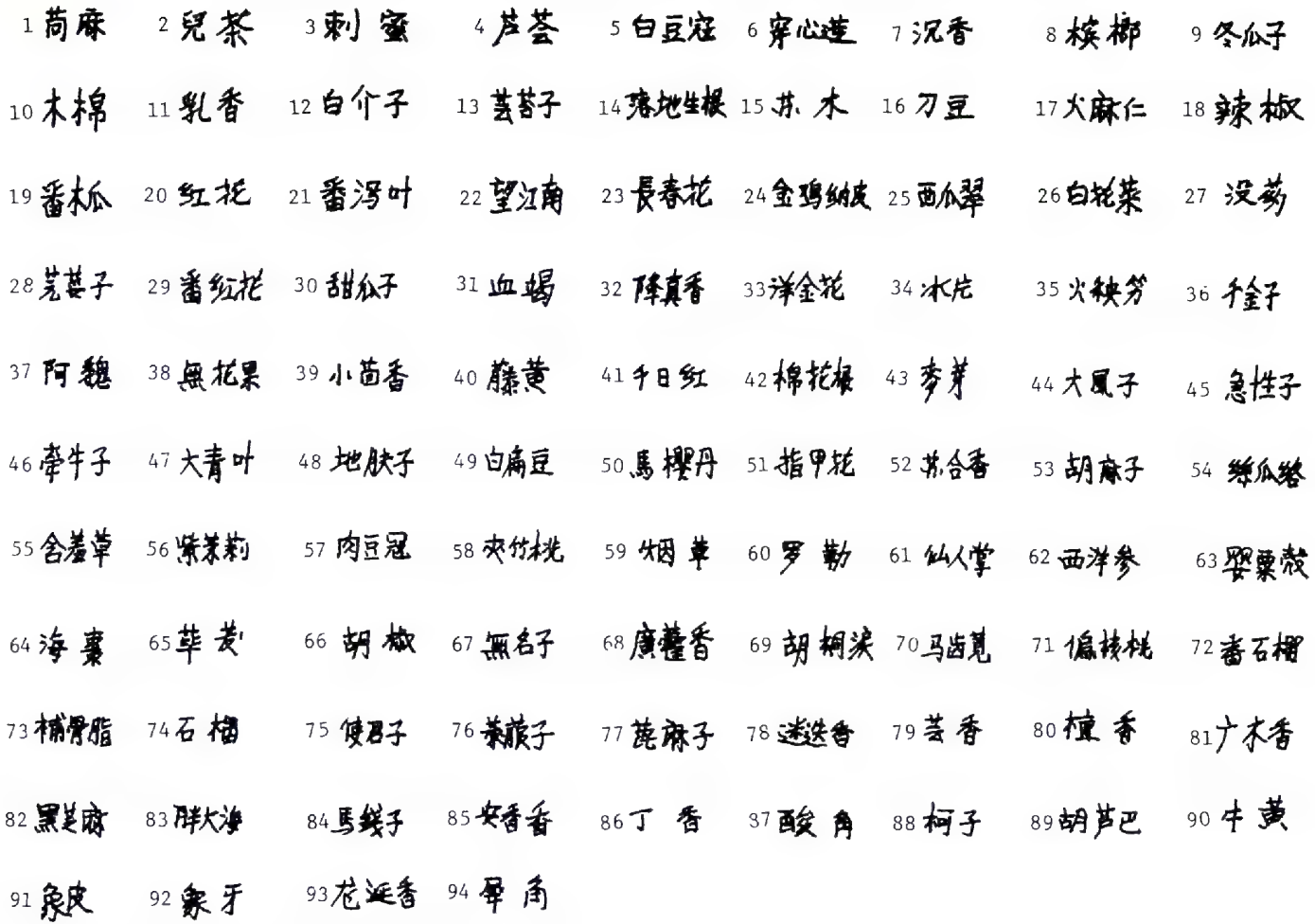
APPENDIX I. **Chinese ideograms of names of exotics used in TCM.***



*The numbers correspond to those given in column two in TABLE 1.

APPENDIX II. **Chinese ideograms of names of ancient herbals and pharmacopoeias.***

1 中药誌
2 中药制劑手册
3 中草药學
4 中药大辞典
5 新華字典
6 陳藏器本草拾遺
7 嵇含南方草木狀
8 蘭茂滇南本草
9 李勣英公唐本草
10 李長傅中國殖民史
11 李時珍本草綱目
12 李珣海药本草
13 劉灝廣群芳譜
14 劉翰茅間宝本草
15 劉恂嶺表錄異
16 倪朱謨本草彙言
17 司馬綏子安集
18 蘇敬唐本草（新修本草）
19 蘇頌图經本草
20 唐慎微証類本草（經史証類備本草，大觀本草，政和經史証類備用本草）
21 陶弘景名医别錄
22 王象晉群芳譜
23 吳其濬植物名实图考 植物名实圖考長編
24 吳普（著述），孫星衍，孫馮翼（校）神農本草經
25 吳儀洛本草從新
26 蕭步丹嶺南採药錄
27 徐國鈞药材學
29 張春樹漢代絲綢之路的開拓與發展
28 嚴用和濟生方
30 掌禹錫嘉祐補註神農本草經
31 趙學敏本草綱拾遺
32 朱橚救荒本草
33 朱震亨本草衍義補遺
34 莊學本增訂嶺南採药錄

*The numbers correspond to those given in LITERATURE CITED. The names of authors are underlined.

PATTERNS OF GEOGRAPHIC DISTRIBUTION AND THEIR IMPLICATIONS ON THE PHYLOGENY OF PUYA (BROMELIACEAE)

G. S. VARADARAJAN[1]

Puya (± 185 species) is widespread at altitudes from sea level to 5000 m and has an extensive range of distribution from Costa Rica to Chile. Previous studies of this genus have been almost entirely taxonomic in nature due to the paucity of field collections and field data. Using extensive field and herbarium data, the present work investigates *Puya* phylogeny based on geographic distributions and cladistic relationships within the genus. Ten geographical regions in the Andean Cordilleras and one region on the Chilean coast constitute centers of diversity where species of *Puya* are concentrated. Allopatric, endemic, or relatively narrow distributions in mountain ranges or valleys suggest that most species were allopatrically derived. Disjunct distributions are evident in a number of allied species and have resulted from vicariance and long-distance dispersal. Several lineages appear to have radiated both vertically (especially in the central Andes) and horizontally (in the northern Andes) during the Pliocene and Pleistocene when climatic and vegetational pulsations were frequent occurrences. A phylogenetic model presented here for *Puya* describes species divergence from the Guayana Highlands to the northern Andes and via the central Andes to Chile. This model emphasizes that while arid cycles generally favored speciation, some episodes in conjunction with uplift of tectonic units caused extinction of lineages.

Puya Molina (± 185 species) is the second largest genus of subfamily Pitcairnioideae of the Bromeliaceae (Varadarajan, 1988). It is widely distributed from Costa Rica to Chile, especially in the Andean Cordilleras. A very small number of species extend eastward into the Guayana Highlands (Guayana) and Amazonian Brazil. Only three other bromeliad genera—*Aechmea* Ruiz & Pavon, *Pitcairnia* L'Hérit., and *Tillandsia* L.—are more widely distributed than *Puya* (L. B. Smith & Downs, 1974, 1977, 1979). Growth forms of *Puya* range from small tuberous herbs to massive palmlike plants (FIGURE 1). Habitats of different species are diverse, occurring from sea level to nearly 5000 m (Varadarajan, 1986, 1988, 1989a; Varadarajan & Gilmartin, 1987).

It has been shown that analysis of geographic distributions often provides interesting insights that aid in discerning the phylogeny of a group (e.g., Humphries, 1981; Platnick, 1981). Despite the extensive distribution of *Puya,* research has not progressed much beyond the level of basic taxonomy (L. B. Smith & Downs, 1974). This situation is due to the paucity of field collections

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Journal of the Arnold Arboretum **71:** 527–552. October, 1990.

FIGURE 1. Diversity of growth forms of *Puya*: a, *P. raimondii,* a remarkable species with a gigantic habit. This flowering individual is nearly 30 feet tall. A massive trunk, formidable spiny foliage, and a columnar inflorescence make it a very conspicuous plant amidst the treeless, rocky habitats of Bolivia. b, *P. trianae,* a small to medium sized (< 1 m) species, presently known from various paramo habitats of Venezuela, Colombia, and Ecuador. c, *P. chilensis,* a species with sympatric populations widespread in several arid localities of Chile. d, *P. brittoniana,* a species attaining 50–60 cm in height; previously

and field data. The complexity within *Puya* is evident from a few recent studies (e.g., Varadarajan, 1987a, 1987b, 1988, 1989a; Varadarajan & Brown, 1988; Varadarajan & Gilmartin, 1988a, 1988b). These studies also emphasize the importance of data from biogeography, pollination studies, ecology, and ecophysiology for elucidating evolutionary phenomena. The principal objectives of this work are to investigate the geographic distributions of various species and examine their inferences on the phylogeny of *Puya*.

METHODS AND OBSERVATIONS

Field and Herbarium Research

Field work for this study has been conducted in Argentina, Bolivia, Chile, Colombia, Ecuador, and Venezuela. The data collected (Varadarajan, 1987a, 1987b, 1988, 1989a) include three major components: descriptive details of the 57 species of *Puya* collected (e.g., growth habit, caudex and foliage type, indumentum morphology, inflorescence morphology, petal color, mode of capsule dehiscence, and estimates of seed number; local distributions of species within their habitats and geographic range (Varadarajan, unpubl. MS); and descriptions of the new species encountered (Varadarajan, 1989b; Varadarajan & Flores, 1990). Field collections consist of plant parts preserved in liquid fixatives and voucher specimens deposited in a number of herbaria (Table 1).

Herbarium collections of 140 species of *Puya* from 25 major herbaria in South America and the United States have also been studied. In many instances my field collections have supplemented the original author's observations and subsequent herbarium data (Varadarajan, 1988, 1989a). Herbarium and field studies were useful for determining precise habitat types, clarifying the taxonomy of some problematical species, estimating overall geographic and/or altitudinal range of species, and understanding the interrelationships between habitats and phenology and their phylogenetic implications.

Habitats

Most species of *Puya* are specific to particular habitat types that range from semixeric to extremely xeric. At high elevations dry mountain slopes, rock outcrops, open grassy and boggy meadows, cloud forests, and paramos include semixeric to moderately xeric habitats. At low elevations savannas and thorn woodlands contain some semixeric habitats. Habitats associated with monte, sierras, punas, and coastal desert vegetation are extremely xeric. A comprehensive account of the habitats of *Puya* is in preparation (Varadarajan, MS).

Phenology

Phenology was studied in selected species of *Puya* and included recognition of distinct stages of morphological change in plants from seed germination

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known only from the type collection, this taxon is sparsely distributed in the punas of Bolivia. A total of only three populations of this species has been encountered by the author during his explorations. (All photographs by the author.)

TABLE 1. **Field collections of Puya made by Varadarajan and associates.**[1]

TAXA	COLLECTION NUMBERS	COUNTRY OF COLLECTION (KNOWN DIVERSITY CENTER)	DISTRIBUTIONAL SUBCLASS
P. aequatorialis André var. *aequatorialis* André	1423, 1426, 1430	Ecuador (IV, V)	1b
P. aequatorialis André var. *albiflora* André	1418	Ecuador (IV, V)	1a
P. aristeguietae L. B. Smith	1188	Venezuela (II)	1c
P. assurgens L. B. Smith[2]	1257	Argentina (X)	1a
P. atra L. B. Smith[2]	1446, 1453	Bolivia (IX)	1a
P. berteroniana Mez	1480, 1482, 1486, 1490, 1492	Chile (XI)	2c
P. brittoniana Baker[2]	1466	Bolivia (VIII)	1a
P. cardenasii L. B. Smith[2]	1442, 1463	Bolivia (IX)	2a
P. castellanosii L. B. Smith[2]	1476	Argentina (X)	1a
P. chilensis Molina	1484, 1488	Chile (XI)	2c
P. clava-herculis Mez & Sodiro	1435, 1436	Ecuador (IV, V)	2b
P. coerulea Lindley var. *coerulea*	1491	Chile (XI)	2b
P. coerulea Lindley var. *intermedia* (Smith & Looser) Smith & Looser	1493	Chile (XI)	2b
P. compacta L. B. Smith[2]	1438	Ecuador (V)	1a
P. ctenorhyncha L. B. Smith[2]	1469	Bolivia (VIII)	1a
P. dyckioides (Baker) Mez var. *dyckioides*	1256, 1475	Bolivia, Argentina (IX, X)	1b
P. dyckioides (Baker) Mez var. *novare* Varadarajan[3]	1477	Argentina (X)	1a
P. ferruginea (Ruíz & Pavón) L. B. Smith	1272, 1278, 1295, 1311, 1448, 1467	Bolivia (VI–IX)	1d
P. floccosa (Linden) E. Morren ex Mez	1170, 1172, 1174, 1175, 1185	Venezuela (I–III)	1d
P. fosteriana L. B. Smith[2]	1464	Bolivia (VIII)	1a
P. gilmartinii Varadarajan & Flores[3]	1481	Chile (XI)	2a
P. glabrescens L. B. Smith	1299, 1300, 1303, 1305, 1307, 1309, 1449	Bolivia (IX)	1c

TABLE 1. **Continued**

TAXA	COLLECTION NUMBERS	COUNTRY OF COLLECTION (KNOWN DIVERSITY CENTER)	DISTRIBUTIONAL SUBCLASS
P. glomerifera Mez & Sodiro[2]	1417	Ecuador (IV, V)	1c
P. hamata L. B. Smith	1422	Ecuador (IV–VI)	2b
P. harmsii (Castellanos) Castellanos[2]	1245	Argentina (X)	1b
P herzogii Wittmack	1301, 1302, 1304	Bolivia (IX)	2a
P. humilis Mez[2]	1298, 1444, 1450, 1451	Bolivia (IX)	2a
P. lanata (HBK.) Schultes[2]	1424	Ecuador (V)	1b
P. leptostachya L. B. Smith[2]	1445	Bolivia (VIII, IX)	1b
P. lilloi Castellanos	1229, 1235, 1264, 1236, 1474	Argentina (X)	1b
P. maculata L. B. Smith[2]	1434	Ecuador (V)	1a
P. meziana Wittmack[2]	1273	Bolivia (VIII)	1b
P. mirabilis (Mez) L. B. Smith	1223, 1226, 1230, 1233, 1237, 1263	Argentina (IX, X)	1d
P. mollis Baker ex Mez[2]	1470	Bolivia (VI–VIII)	1d
P. nana Wittmack[2]	1461	Bolivia (IX)	1a
P. nutans L. B. Smith[2]	1429, 1432	Ecuador (V)	2a
P. pearcei (Baker) Mez[2]	1286, 1291, 1447, 1472	Bolivia (VIII, IX)	1b
P. pygmaea L. B. Smith[2]	1428, 1437	Ecaudor (V)	2a
P. raimondii Harms	1465	Bolivia (VII–IX)	1b
P. retrorsa Gilmartin[2]	1419, 1420, 1440, 1441	Ecuador (between IV & V)	1b
P. riparia L. B. Smith	1274, 1275, 1276	Bolivia (VIII)	1a
P. sanctae-crucis (Baker) L. B. Smith var. *sanctae-crucis*	1454, 1457, 1458	Bolivia (VIII, IX)	1b

TABLE 1. **Continued**

TAXA	COLLECTION NUMBERS	COUNTRY OF COLLECTION (KNOWN DIVERSITY CENTER)	DISTRIBUTIONAL SUBCLASS
P. sanctae-crucis (Baker) L. B. Smith var. *verdensis* Varadarajan[3]	1459	Bolivia (IX)	1a
P. smithii Castellanos	1479	Argentina (X)	1b
P. sodiroana Mez[2]	1427, 1431	Ecuador (V)	2a
P. solomonii Varadarajan[3]	1471	Bolivia (VIII)	1b
P. spathacea (Grisebach) Mez	1240, 1243, 1268	Argentina (outside of X, XI)	1b
P. stenothyrsa (Baker) Mez	1310, 1312, 1468	Bolivia (VIII)	1b
P. trianae Baker[2]	1189, 1439	Venezuela, Ecuador (II, III, V)	1d
P. tristis L. B. Smith[2]	1306, 1308	Bolivia (IX)	2a
P. tuberosa Mez[2]	1455	Bolivia (IX)	1a
P. tunarensis Mez[2]	1296, 1452	Bolivia (IX)	2b
P. ultima L. B. Smith[2]	1277	Bolivia (VIII)	1a
P. ushae Varadarajan[3]	1460	Bolivia (IX)	1a
P. venusta Philippi	1483, 1487	Chile (XI)	2b
P. yakespala Castellanos[2]	1478	Argentina (X)	1a
P. zakiana Varadarajan[3]	1425	Ecuador (V)	1a

[1] Voucher specimens housed in one or more of the following herbaria: GH, LAP, LPB, MO, NY, PORT, SALT, SEL, US, VEN, WS; for details of diversity centers and distribution classes see text.

[2] Taxa previously known from five specimens or fewer.

[3] New taxa encountered.

TABLE 2. **Most commonly observed patterns of phenology in polycarpic species of Puya.**[1]

PHENOLOGICAL CHARACTERISTICS RECORDED	PATTERNS OF SEASONAL PHENOLOGICAL CHANGES	
	SPECIES IN LOWER LATITUDES[2]	SPECIES IN SOUTHERN LATITUDES[3]
Seed germination and vegetative growth	Completed in 1–5 years	Completed in 1–5 years
Initiation of scape	February	September
Differentiation of inflorescence	↓	↓
Initiation of flowers		
Differentiation of flowers		
Anthesis		
Pollination	September	February
Fruit set	October	March
Seed development	↓	↓
Capsule maturation and dehiscence		
Seed dispersal	January	August

[1] Nonseasonal phenological changes are irregular, not synchronized with seasons; some years are characterized by much longer periods of vegetative growth and others by greatly extended periods of flowering and fruiting (examples: *Puya pearcei, P. stenothyrsa*). Successive (complex) phenological changes occur in sympatric groups where the changes are not synchronized with yearly seasons (examples: *Puya clava-herculis, P. nutans,* and *P. pygmaea*).

[2] Example: *Puya retrosa.*

[3] Example: *Puya spathacea.*

through seed dispersal (TABLE 2). There appears to be an interesting correlation between phenology and geographic distribution, especially in the following contexts: (a) sympatric species groups; (b) overlapping species distributions within the same geographical range; and (c) occasional sympatric distribution of predominantly isolated species.

Species of *Puya* are perennial, and with a few exceptions all are polycarpic. Phenology of monocarpic species is well illustrated by *P. raimondii* (FIGURE 1). This gigantic species continues to grow vegetatively for seven to ten years. The transition from a vegetative to the reproductive phase appears to be somewhat abrupt, yet the flowering period lasts for up to three years. The nearly twelve-foot tall, indeterminate inflorescence tends to grow rather rapidly after it attains three to four feet in height. The final phase of inflorescence growth, however, appears to be gradual. Although seeds are abundantly produced (about 400 seeds estimated per capsule), the germination rate is extremely low (< 1%). The seed remains dormant for nearly two years.

Polycarpic species exhibit at least three distinct phenological patterns (TABLE 2). In some species (e.g., *Puya spathacea* and *P. mirabilis*) phenological cycles synchronize with yearly seasonal changes. While the phenological pattern is nonseasonal in some widespread species (e.g., *P. ferruginea*), it is complex in others. The following group of co-occurring species in Ecuador illustrates one complex pattern. Within the assemblage of *P. clava-herculis, P. nutans,* and *P.*

pygmaea, P. pygmaea begins its early reproductive phase (inflorescence differentiation) when *P. clava-herculis* enters the final reproductive phase (fruit and seed setting), but *P. nutans* remains in a vegetative phase.

ANALYTICAL RESEARCH

Results of the analysis of herbarium and field data are presented in the following section, and some are summarized on the MAP and in FIGURES 2–4. Phylogenetic interpretations of *Puya* are founded on the individual species distributions, species subsets, their putative cladistic relationships, and similar data known for organisms occurring in the same region.

Geographic Distributions

The principal objective in analyzing the distributions of *Puya* was to recognize specific geographic regions where multiple species are concentrated. This was done by mapping the sites of occurrence of every species. Regions that contain five to forty species are circumscribed here as centers of diversity (see MAP). The area of each diversity center ranges approximately from 12,000–25,000 km^2.

Cladistic Analysis

A series of procedural steps were involved in the cladistic analysis of various species of *Puya*. The first step was to delimit tentative monophyletic subsets or groups of species and analyze these subsets together in order to reconstruct the phylogeny of the genus. In addition to species subsets, several isolated taxa that did not associate with other individuals or species groups became evident. These isolated taxa displayed only autapomorphies. Monophyletic species subsets recognized here by synapomorphies are of two categories: (1) allied pairs of species that occupy putative terminal branches within a larger (somewhat unresolved) cladogram, and (2) alliances of three to several species that constitute a principal lineage.

Three principal sources aided in my initial choice of species subsets for the analysis. First, the diagnostic key to species of Smith and Downs (1974) suggested a number of pairs or groups of taxa that share multiple characters. Several of these polythetic groups were tested (Sanders, 1981; Wiley, 1981) and were found to be monophyletic (e.g., *Puya* subgenus *Puya*). Second, my continued observations of various developmental stages of species in the field, supplemented by herbarium studies, provided a better definition of some morphological traits (e.g., inflorescence, indumentum). This approach allowed me to recognize additional monophyletic species subsets (e.g., the *Puya tuberosa* complex). Third, a re-examination of several previously neglected, unusual characters (e.g., lustrous bracts, caudex) suggested a few more monophyletic species assemblages.

Data bases with usually less than ten characters were prepared for the subsets of *Puya*. The ancestral and derived states of these characters were determined

MAP. Geographic locations of centers of diversity of *Puya*. The approximate latitudinal and longitudinal limits of each center are given in parentheses. For other details see text. I, Sierra Nevada de Santa Marta (10°5′–11°2′ N, 73°2′–74°2′ W); II, eastern cordillera of Colombia and Mérida Andes (5°8′–8°5′ N, 71°6′–73°3′ W); III, Cundinamarca (4°–5°5′ N, 73°3′–75° W); IV, southwestern Colombia and northern Ecuador (0°–36′ N, 76°–78°3′ W); V, south-central Ecuador (2°–4° S, 78°5′–79°5′ W); VI, northern Peru (6°–8° S, 77°–79°2′ W); VII, central Peru (9°2′–12° S, 75°–77°2′ W); VIII, Titicaca (13°6′–17° S, 67°5′–72° W); IX, southern Bolivia (16°5′–21°5′ S, 63°3′–66°7′ W); X, northwestern Argentina (22°3′–28° S, 64°–67°8′ W); XI, Chile (26°–36°5′ S, 69°–72°8′ W).

by the outgroup method (Stevens, 1980; Watrous & Wheeler, 1981). Cladograms were manually constructed in accordance with the procedures discussed by Sanders (1981). Provisional outgroup for the species of *Puya* subgenus *Puya* could be any species of the putative sister taxon, *Puya* subgenus *Puyopsis*. Morphological and/or distributional criteria provided the basis for the choice of outgroups for the other species subsets recognized.

RESULTS

Results of the distributional data and of the cladistic analysis address three important questions. Which geographic regions are characterized by relatively high concentration of species? What patterns do these distributions underlie? What is the correlation between geographic distributions and suggested cladistic affinities of species? Each question is discussed below.

CENTERS OF DIVERSITY

All the geographic regions that constitute the following eleven centers of diversity of *Puya* are in South America (see MAP). Center I (Sierra Nevada de Santa Marta) is the most northern and isolated unit of the Andes in Magdalena region in northern Colombia. Center II (eastern cordillera of Colombia and Mérida Andes) covers the northeastern section of Colombia between Norte de Santander and Boyaca, and neighboring Venezuela including Táchira, Mérida, and Trujillo regions. Center III (Cundinamarca) consists of the central part of the eastern cordillera of Colombia. Center IV (southwestern Colombia and Northern Ecuador) includes the territory approximately between the area where the three Andean Cordilleras are divided (Valle del Cauca, Nariño in Colombia) and the volcanic sites of Imbabura in northern Ecuador. Center V (south-central Ecuador) extends between the Cañar and Zamora regions. Center VI (northern Peru) encompasses part of the lowlands of the Amazonas and San Martín regions and the Cordillera Oriental of the Peruvian Andes in the Cajamarca and La Libertad regions. Center VII (central Peru) lies between the Ancash and Ayacucho regions, mainly along the Cordillera Oriental. Center VIII (Titicaca) includes the Cordillera Oriental and Altiplano. It stretches across Lake Titicaca between the Apurimac-Arequipa regions in Peru and the La Paz region in Bolivia. Center IX (southern Bolivia) consists of the eastern part of the Altiplano and the adjoining Cordillera Oriental covering the Cochabamba, Chuquisaca, Potosi, and Tarija regions. Center X (northwestern Argentina) covers the Salta and Jujuy regions. Center XI (Chile) extends between the Antofagasta in the north to Bío Bío in the south.

Center I contains the lowest number of species (five), while centers VII, VIII, and IX harbor the highest species number (nearly forty). All but center XI encompass extensive altitudes (800–5000 m), while center XI includes a much smaller range (sea level to approximately 2000 m). Each center is separated from the closest adjacent one by a distance of at least 200 km. Nearly 75% of the species of *Puya* occur within one or more of the diversity centers circumscribed here, and some species occupy two to three adjacent centers (e.g., *P. clava-herculis, P. dyckioides,* and *P. hamata*) as well as occurring in the intervening areas (e.g., *P. ferruginea.*) Rarely, a few species occur only in the interdiversity regions (e.g., *P. retrorsa* and *P. spathacea*).

DISTRIBUTION PATTERNS

Geographical distributions of species of *Puya* are allopatric and sympatric (TABLE 3).

TABLE 3. **Key characteristics of the distributional classes of Puya.**

DISTRIBUTION CLASS AND SUBCLASS	STANDS	NO. OF INDIVIDUALS PER STAND (AVERAGE)	OCCURRENCE WITHIN DIVERSITY CENTER(S)	EXAMPLES
1. **Allopatric**				
a. Locally endemic	Usually single	<15	Confined to 1 center	*P. castellanosii*
b. Locally widespread	Multiple	20–30	1 or more centers	*P. lilloi*
c. Predominantly allopatric, widespread, occasionally sympatric	Multiple allopatric and single sympatric	<15	Typically in 1 center; sometimes 2 adjacent centers	*P. glabrescens*
d. Allopatric with extensive distributions	Multiple	30–50	Always in more than 1 center	*P. floccosa*
2. **Sympatric**				
a. Locally endemic, sympatric	Single	<15	Confined to 1 center	*P. nutans, P. pygmaea,* & *P. sodiroana*
b. Nonendemic, sympatric	Multiple	15–30	1 or more centers	*P. bicolor, P. goudotiana,* & *P. lineata*
c. Nonendemic, replicate sympatric	Multiple	Variable	1 center	*P. berteroniana, P. chilensis, P. gilmartinii,* & *P. venusta*

Allopatric Distributions

Allopatric distributions are characterized by conspecific populations or population systems in diverse, geographically widely separated habitat types. Nearly two-thirds of the species of *Puya* are allopatric on mountain slopes and in valleys, and about one-half are narrow (local) endemics. The range and pattern of species distribution within diversity centers serve as secondary criteria for recognizing subclasses of allopatry.

1a. ALLOPATRIC, LOCAL ENDEMICS (TABLE 3). Allopatric species that are also local endemics occupy relatively few stands but are known from all diversity centers. Distributional territories of these allopatric species are usually restricted to peripheral parts of a diversity center where other species are notably absent. *Puya brittoniana* (FIGURE 1), *P. castellanosii,* and *P. yakespala* illustrate these typical features. The first species comprises a total of three population systems within a radius of about 25 km in the punas of western Bolivia (center VIII). The three known populations of *P. castellanosii* are native to the Cachi, Molinos, and Brealito sites at about 3000 m elevation in the Calchaquies valleys in northwestern Argentina (center X), while *Puya yakespala* is known only from a single population system in the Yakespala puna slopes of northwestern Argentina at about 4000 m elevation (center X).

1b. ALLOPATRIC, LOCALLY WIDESPREAD (TABLE 3). Allopatric species may be locally widespread in one or two diversity centers. *Puya pearcei*—a good example of a species with multiple stands—is known from cloud forests and cloud forest-puna transitional zones in centers VIII (La Paz region) and IX (Chapare region). *Puya spathacea,* native to north-central Argentina, also conforms to the typical features of this subclass. However, its distribution pattern appears to be somewhat peculiar since the territory of this species is situated several hundreds of kilometers outside of centers X and XI, where other species of *Puya* are not known to exist. *Puya raimondii* (FIGURE 1) is yet another example of this subclass. This allopatric species consists of disjunct multiple stands in centers VIII and IX, which are separated from one another by great distances.

1c. WIDESPREAD, PREDOMINANTLY ALLOPATRIC, AND OCCASIONALLY SYMPATRIC (TABLE 3). When allopatric species consist of multiple stands, some stands may be sympatric with other species within a single diversity center. Species of this subclass (e.g., *Puya glabrescens,* center XI) include fewer individuals per stand in sympatric sites than in allopatric sites. Allopatric sites are found at mid-elevations among low montane forests, while sympatric sites are in the subalpine to alpine vegetations at higher elevations. Species native to sympatric sites are narrow endemics. *Puya glabrescens* has allopatric populations in scrub forests (2000–2500 m); it is sympatric with *P. herzogii* (Mount Tunari region), *P. humilis* and/or *P. tunarensis* (Pojo region) in various puna habitats (3500–4000 m).

1d. ALLOPATRIC WITH EXTENSIVE DISTRIBUTIONS (TABLE 3). Very few allopatric species (e.g., *Puya floccosa, P. ferruginea,* and *P. mirabilis*) are widespread in two or more diversity centers. Notable characteristics of these species are large

population size (with at least 50 individual plants per population) and extensive intra-population variability. In terms of territory and altitude, the distribution of *P. floccosa* is unmatched by any other member of the genus. This species extends from Costa Rica to Colombia in the Andes (centers I–III), and eastward into the Venezuelan/Brazilian Guianas where its altitudinal range is approximately 3000 m. There are two morphological variants of *P. floccosa*. *Puya ferruginea* is known from southern Ecuador to central Bolivia (centers V–IX). At least two distinct population systems of *P. ferruginea* occur at mid-elevations, each characteristic of cloud forests and highly arid alpine vegetation. *Puya hamata* (centers IV–VI) and *P. mirabilis* (centers IX–X) are also widely distributed in multiple diversity centers.

Sympatric Distributions

Sympatric distributions are characterized by an assemblage of two or more species whose populations or population systems share the same habitat type. About 10–15% of the species of *Puya* appear to be typically sympatric. Spatial distributions of individual species in a common habitat present some variations. Sometimes conspecific populations of sympatric species are intermingled with one another in the same habitat without clear boundaries (e.g., *P. chilensis, P. coerulea,* and *P. venusta* in center XI). By contrast, some sympatric groups (e.g., *P. aristeguietae* and *P. trianae,* in center II) occur only in isolated stands within a habitat. The extent of distributions of the individual taxa and some putative cladistic relationships within the members of the sympatric group provide variations for recognizing subclasses in this category.

2a. Locally endemic sympatric species (Table 3). Endemic sympatric species of this subclass are characterized by narrow distributional ranges. Each species may have few to several isolated stands. Individual plants of a stand are sparsely spaced within the habitat. *Puya compacta, P. nutans, P. pygmaea,* and *P. sodiroana* are sympatric and locally endemic to a few paramos of Ecuador (center V, Azuay Province). The habitats of *P. compacta* and *P. sodiroana* are dry slopes whereas those of the other species are swampy meadows.

2b. Non-endemic sympatric species (Table 3). Typically, species of this subclass occur in one or two contiguous centers in various sympatric combinations. For instance, *Puya bicolor* Mez, *P. goudotiana* Mez, *P. lineata* Mez, and *P. trianae* (Figure 1) are sympatric in a paramo site in center III. However, in other areas of center III, *P. bicolor, P. cleefii* L. B. Smith & Read, and *P. santosii* Cuatrecasas are sympatric. *Puya goudotiana* is sympatric with either *P. killipii* Cuatrecasas or *P. santanderensis* Cuatrecasas in center II. *Puya lineata, P. nitida* Mez, and *P. santosii* are sympatric in various sites of center III. *Puya trianae*—perhaps the most widespread among the sympatric species—is sympatric with *P. aristeguietae* and *P. cardonae* L. B. Smith in center II, and *P. clava-herculis* and *P. pygmaea* in center V.

2c. Non-endemic, replicate sympatric species groups (Table 3). A group of fairly widespread species may be found together repeatedly in several sites. One species group in Chile illustrates this subclass. *Puya alpestris* Poeppig, *P.*

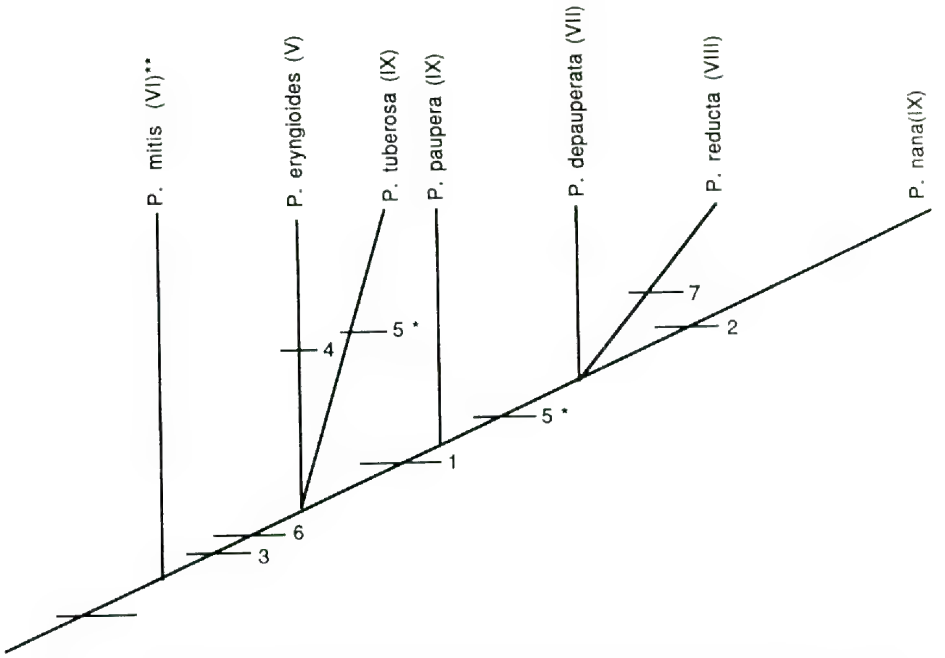


FIGURE 2. Cladogram of the *Puya tuberosa* complex. The outgroup (*P. mitis* Mez) and the ingroup share an apomorphy (dwarf growth habit) against *P. wurdackii* (plants 1 m tall or taller). Roman numerals indicate diversity centers, arabic numerals signify apomorphies of characters; single asterisks indicate homoplasies and double asterisks, outgroups. Data matrix and characters for taxa included are presented in TABLE 4.

berteroniana, P. boliviensis Baker, *P. gilmartinii,* and *P. chilensis* (FIGURE 1) occur in various combinations and are encountered in several localities (see below). *Puya berteroniana* and *P. chilensis* are the most frequent species in any sympatric assemblage. Similar replicate sympatric groups appear to be rare in *Puya.*

CLADISTIC ANALYSIS AND DISTRIBUTIONS

The results of cladistic analysis may be examined from a distributional perspective of the various members of a monophyletic group. Conversely, the distributional data may also be described from a cladistic perspective of sympatric groups.

The *Puya tuberosa* complex (FIGURE 2; TABLE 4) illustrates a monophyletic group in which the individual sister taxa are allopatric and geographically separated by great distances. This subset of *Puya* is found in several diversity centers, although the individual species are locally endemic to particular centers (subclass 1a). Sister species of this subset as well as other groups are geographically disjunct by distances of a few to several hundred kilometers (TABLE 5).

The monophyletic group *Puya* subgenus *Puya* (FIGURE 3; TABLE 6) reveals some interesting distribution pattern types. A part of this group in center XI consists of replicate sympatric species (subclass 2c; e.g., *P. alpestris* and *P.*

TABLE 4. **Data matrix of Puya tuberosa complex and its outgroup.**

SPECIES	CHARACTERS[1]						
	1	2	3	4	5	6	7
P. mitis	A	A	A	A	A	A	A
P. eryngioides	A	A	B	B	A	B	A
P. depauperata	B	A	B	A	B	B	A
P. paupera	B	A	B	A	A	B	A
P. nana	B	B	B	A	B	B	A
P. reducta	B	A	B	A	B	B	B
P. tuberosa	A	A	B	A	B	B	A

[1] List of characters: 1, underground rhizome/bulb (A) present, (B) absent; 2, scape (A) lax and conspicuous, (B) condensed and short; 3, inflorescence (A) simple, (B) compound; 4, flowers (A) pedicellate, (B) subsessile; 5, floral bracts (A) toothed, (B) entire; 6, flowers (A) nodding, (B) erect; and 7, scape bracts (A) membranous to coriaceous, (B) chartaceous.

chilensis in the Bío Bío region; *P. berteroniana* and *P. chilensis* in the Coquimbo and Valparaiso regions; *P. berteroniana, P. boliviensis, P. chilensis,* and *P. gilmartinii* in the Atacama-Antofagasta regions). *Puya berteroniana* may also be allopatric along the dry slopes of the Andes (ca. 2000 m). *Puya castellanosii* and *P. weddeliana* are allopatric, local endemics (subclass 1a) while the allopatric *P. raimondii* consists of disjunct multiple stands.

Locally endemic sympatric groups and non-replicate assemblages do not include cladistically closely related taxa. Non-replicate sympatric groups differ from site to site. Cladistic analysis of the sympatric group including *Puya bicolor, P. goudotiana,* and *P. lineata* (subclass 2b) indicates affinities for each taxon with allopatric species characterized by narrow distributions and wide geographical disjunctions (FIGURE 4).

TABLE 5. **Examples of geographically allied disjunct species pairs in Puya.**

SPECIES	DIVERSITY CENTER(S)
Species disjunct in contiguous centers	
P. aristeguietae and *P. goudotiana*	II & III
P. killipii and *P. nitida*	
P. micrantha and *P. pearcei*	IX & X
P. fosteriana and *P. weberiana*	
P. castellanosii and *P. chilensis*	X & XI
P. coerulea and *P. smithii*	
Species with major disjunctions	
P. floccosa and	I–III
P. spathacea	outside of X & XI
P. nivalis and	I
P. yakespala	X
P. nutans and	V
P. venezuelana	II

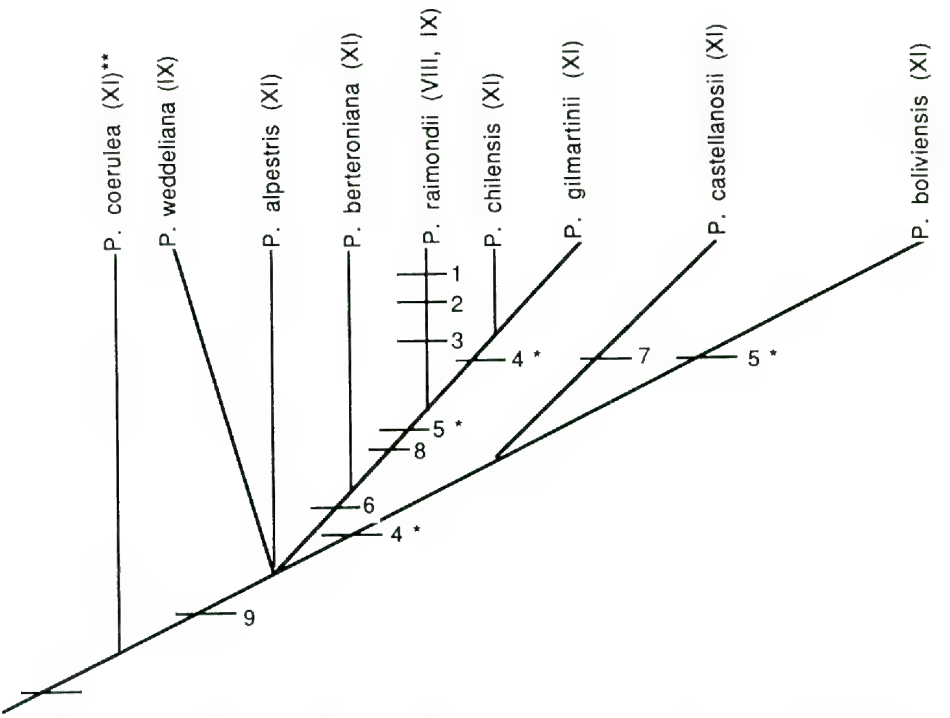


FIGURE 3. Cladogram of *Puya* subgenus *Puya*. The outgroup (*P. coerulea*) and the ingroup share an apomorphy (spirally twisted postanthesis petals) against *Pitcairnia paniculata* (Ruiz & Pavon) Ruiz & Pavon (straight postanthesis petals). Roman numerals indicate diversity centers, arabic numbers signify apomorphies of characters; single asterisks indicate homoplasies and double asterisks, outgroup. Data matrix and characters for taxa included are presented in TABLE 6.

DISCUSSION

Results of the analyses of geographic distributions and cladistic relationships among species of *Puya* provide insights into the phylogenetic history of divergence lineages and some likely causes and consequences. In addition, these results suggest that a number of species were allopatrically derived. Restricted occurrence and habitat specificity of many species indicate that the isolating mechanisms are geographical. The paraphyletic or polyphyletic nature of most sympatric groups reflects local radiations of several independent phyletic lineages within a geographic center. There is no direct evidence for hybridization of species within the sympatric complexes. Mechanisms that isolate these sympatric species are likely to be genetic.

PHYLOGENETIC HISTORY OF DIVERGENCE OF SPECIES OF PUYA

The literature on the neotropical climatic and vegetational history in conjunction with the geographic distribution of species, habitats, and diversity centers of *Puya* allows for a presentation of a model of phylogenetic divergence of various species lineages. This phylogenetic model emphasizes some likely

TABLE 6. **Data matrix of Puya subgenus Puya and its outgroup.**

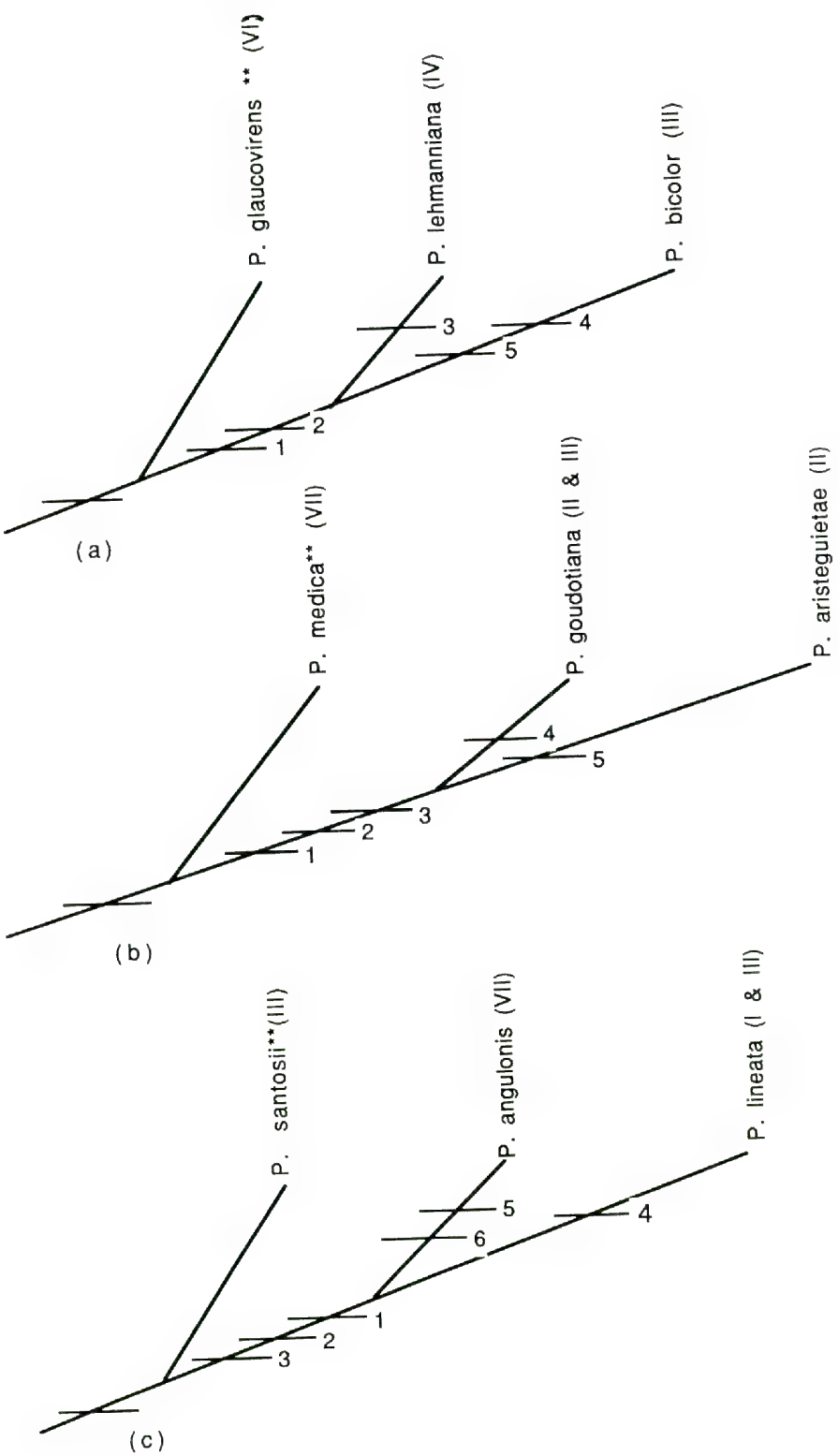
SPECIES	CHARACTERS[1]								
	1	2	3	4	5	6	7	8	9
P. coerulea	A	A	A	A	A	A	A	A	A
P. raimondii	B	B	B	A	B	B	A	B	B
P. weddeliana	A	A	A	A	A	A	A	A	B
P. castellanosii	A	A	A	B	?	A	B	A	B
P. chilensis	A	A	A	B	B	B	A	B	B
P. alpestris	A	A	A	A	A	A	A	A	B
P. boliviensis	A	A	A	B	B	A	A	A	B
P. gilmartinii	A	A	A	B	B	B	A	B	B
P. berteroniana	A	A	A	A	A	B	A	A	B

[1] List of characters: 1, caudex (A) noncolumnar, often prostrate, (B) stout and columnar; 2, plants (A) polycarpic, (B) monocarpic; 3, leaf rosette (A) at ground level, (B) above ground level; 4, leaf blades (A) with strongly contrasting surfaces (at least in part), (B) concolorous; 5, petals (A) blue/blue-green, (B) yellow/yellow-green/greenish white; 6, inflorescence branches (A) numbering 30 or less, (B) numbering 80 or more; 7, inflorescence indument (A) nonferruginous, (B) ferruginous; 8, floral bracts (A) distinctly exceeded by sepals, (B) equaling or exceeding sepals; and 9, sterile apex in inflorescence (A) absent, (B) present.

routes of divergence from a previously proposed geographical region of primary differentiation.

Initial Divergence

Diversity centers of *Puya* from I to X are confined to the Andes, and center XI is in Chile (MAP). Characteristic species habitats within these centers indicate that divergence of many lineages occurred principally in paramos (northern Andes), punas (central Andes), and coastal deserts (Chile). We know from recent studies (Varadarajan, 1986; Varadarajan & Gilmartin, 1988a) that the genera of the Pitcairnioideae evolved in the Guayana, and some of them (e.g., *Pitcairnia* and *Puya*) later expanded in the Andes. It is intriguing, however, that species of *Puya* are abundant only in the moderately to extremely xeric habitats of the Andes and not in the semixeric habitats of the Guayana. At least two explanations warrant consideration in this connection. The first explanation contends that only a few species evolved in the Guayana prior to a major proliferation in the Andes. This idea is concurrent with the preponderance of more diverse xeric habitats in the Andes than in the Guayana (Sarmiento, 1975). According to the second explanation, the ancestral lineages of *Puya* in the Guayana were essentially semixeric, occupying such habitats as sandstone bluffs, talus slopes, and igneous "lajas." The moderately xeric lineages in the Andes descended from the semixeric ones and invaded extremely xeric sites at high elevations. This hypothesis also rests on the assumption that several semixeric or moderately xeric lineages became extinct in the Guayana as a result of a series of catastrophic environmental changes (van der Hammen, 1982), some of which were reflected in the frequent contraction and expansion of savannas (Huber, 1982). During comparable time periods, however, the Andean regions experienced more or less equitable environments that were


P. glaucovirens ** (VI)
P. lehmanniana (IV)
P. bicolor (III)
1
2
3
4
5
(a)
P. medica** (VII)
P. goudotiana (II & III)
P. aristeguietae (II)
1
2
3
4
5
(b)
P. santosii**(III)
P. angulonis (VII)
P. lineata (I & III)
1
2
3
4
5
6
(c)

congenial to the survival and proliferation of the descendant lineages (see van der Hammen, 1982, for related discussions).

Colonization and Diversification in the Northern Andes

Two migratory routes may have been important for the radiation of *Puya* from Guayana into the Andes. The first was via the eastern highlands of Colombia into the northern Andes of Colombia and Ecuador (centers II to IV); the second was via the Peruvian Amazon region into the central Andes (centers VI to VIII).

Guayana, an expansive floristic province of South America (Steyermark, 1982), is characterized by its underlying sedimentary mantle (Roraima) that constitutes most of the highlands. The mantle stretches out into eastern Colombia in a series of isolated "mesitas," adjoining the Cordillera Macarena and the flanks of the Andes (Maguire, 1970). The physical contiguity between Guayana and the Andes may have facilitated a direct migration of some Guayanan species of *Puya* into the Colombian Andes (eastern Cordillera, centers II and III).

The distribution of a sizable number of species of *Puya* in the paramos and the adjoining subparamos and montane habitats (elevations 2000 m and above) would be important in the context of divergence. A plausible explanation may be that at lower elevations species initially invaded the montane forest habitats and subparamos, from which they migrated to the paramos at high elevations. These migrations were probably best suited to glacial periods. During glacial times paramo areas were geographically much expanded, and the intervening distances between them were much reduced. This physio-geographic situation, combined with a massive production of wind-dispersed seeds, facilitated extensive colonization by several species. During interglacial periods, on the

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FIGURE 4. Cladograms of the members of a sympatric species group (*Puya bicolor, P. goudotiana,* and *P. lineata*). a, Alliance of *Puya bicolor.* The outgroup (*P. glaucovirens*) and the pair of sister species share an apomorphy (stout pedicels) against *P. adscendens* L. B. Smith (slender pedicels). Polarity is established in the following characters: 1, dry inflorescence axes: angled to cylindrical; 2, racemes: polystichously flowered to densely flowered toward apex; 3, sepals: symmetric to asymmetric; 4, flowers: erect to downwardly secund; 5, primary bracts: shorter than or equalling sterile bases of racemes to longer than sterile bases of racemes. b, Alliance of *P. goudotiana.* The outgroup (*P. medica*) and the pair of sister species share an apomorphy (petals 4 cm long or longer) against *P. phelpsiae* L. B. Smith (petals 2–5 cm long or smaller). Polarity is established in the following characters: 1, scape bracts and primary bracts: persistent to disintegrating rapidly after anthesis; 2, primary bracts: pectinate-serrate to entire; 3, sepals: carinate to ecarinate; 4, flowers: erect-spreading to recurved; 5, petals: blue-bluish green to white. c, Alliance of *P. lineata.* The outgroup (*P. santosii*) and the pair of sister species share an apomorphy (very densely imbricate scape bracts) against *P. laccata* Mez (lax scape bracts). Polarity is established in the following characters: 1, inflorescence: compound to simple; 2, floral bracts: entire to pectinate-serrate; 3, floral bracts: not lustrous to lustrous; 4, sepals: obtuse to apiculate; 5, sepals: not lustrous to lustrous; 6, pedicels: simple to compound and winged. Roman numerals indicate diversity centers, arabic numbers signify apomorphies of characters; single asterisks indicate homoplasies and double asterisks, outgroups.

contrary, paramos were fragmented into discrete "islands" in which isolation was followed by speciation (for related discussions see Cleef, 1979; Cuatrecasas, 1957, 1979; van der Hammen, 1974, 1979, 1982).

The Sierra Nevada de Santa Marta deserves mention in this discussion. While it constitutes the northernmost and geographically the most ancient structural unit of the Andes (Simpson, 1975), the Sierra Nevada de Santa Marta may not necessarily have been a region of initial invasion by species of *Puya*. This suggestion is based on the contemporary idea of Guayanan differentiation of the genus and on the lack of direct geological and ecological continuity between Guayana and the Sierra Nevada de Santa Marta. These floristic provinces are separated by a region of predominantly mesic communities—the "llanos" and the adjoining mosaics of low vegetation—that historically separated xeric species of some plant families between the Andes and Guayana (see Steyermark, 1982). The latter situation is true for *Puya* as well. This suggests that the Sierra Nevada de Santa Marta may be a refuge area for species of *Puya* where taxa were dispersed from centers II and/or III. Subsequently, they became isolated as a result of unusually long dry periods and unique geological events. Preliminary assessments of phyletic relationships suggest relictual status for the species of *Puya* native to the Sierra Nevada de Santa Marta.

Expansion in the Central Andes

The Amazonian lowlands, including pockets of xeric habitats, have perhaps provided geographical continuity between Guayana and the eastern slopes of the Peruvian and Bolivian Andes. The lineages that initially colonized these low Andean habitats further extended into high elevation punas and adjoining arid regions. A substantial number of lineages seem to have proliferated in the alpine regions of Peru and Bolivia (centers VII and VIII). Present evidence suggests that at least some of these high elevation lineages have descended directly from the lower elevation species (TABLE 7). The process of radiation and differentiation in the central Andes probably occurred at different times during glacial cycles than did similar events in the northern Andes. Specifically, glacial periods in the central Andes saw the development of significant water barriers across the Altiplano as a result of the presence of a massive system of lakes and rivers; these water barriers fragmented habitats and led to population isolation and speciation (Simpson, 1975; Varadarajan, 1986; Varadarajan & Gilmartin, 1988a). In the northern Andes, by contrast, speciation events occurred during interglacial times.

Radiation into Chile

There are at least three central Andean ancestral sources for the species lineages now native to Chile. The present distributional and cladistic analyses of *Puya* subgenus *Puya* (FIGURE 3) suggest that these ancestral taxa (similar to *P. raimondii, P. weddeliana,* and *P. castellanosii*) may have been from centers VIII, IX, or X (MAP). A vicariance model (see below) is conceivable for the differentiation of *Puya* subgenus *Puya* in light of some available evidence (TABLE 4).

TABLE 7. **Examples of high altitude species of Puya and their lower altitude allies.**

HIGH ALTITUDE TAXA			ALLIED LOWER ALTITUDE TAXA			
Species	**Altitudinal range (in m)**	**Vegetational type**	**Species**	**Altitudinal range (in m)**	**Vegetational type**	**Diversity center**
P. harmsii (Castellanos) Castellanos	3000–3600	Monte, punas	*P. lilloi* Castellanos	800–2000	Transitional forests	X
P. dyckioides (Baker) Mez	1300–4000	Scrub, punas	*P. assurgens* L. B. Smith	1800–2000	Low scrub forests	X
P. weberbaueri Mez	2800–4000	Punas	*P. lasiopoda* L. B. Smith	500–2300	Moist forests	VIII

CONVERGENT EVOLUTION IN PUYA

The distribution of habitats (punas, coastal deserts, etc.) within diversity centers suggests evolution of most species of *Puya* under the regime of arid environments. This notion is well attested to by a number of structural (Robinson, 1969; Tomlinson, 1969; Varadarajan, 1986; Varadarajan & Gilmartin, 1987) and physiological (Medina, 1974; Medina *et al.*, 1977; Griffiths, 1984; Griffiths & J. A. C. Smith, 1983; J. A. C. Smith *et al.*, 1986) features. It is important to note that these features are by no means confined to a single phyletic lineage. Climatic history of the Andes (e.g., Simpson, 1975; van der Hammen, 1974) indicates the occurrence of several independent episodes of arid cycles during Pliocene and Pleistocene times when various regions experienced frequent climatic and vegetational pulsations and the uplift of tectonic plates. For example, in the intermountain valleys of the northern Andes xeric environments developed as a result of mountain barriers, which produced rain shadow effects by intercepting the movement of wet air masses (Gilmartin, 1973; Sarmiento, 1975). In coastal areas, however, aridity resulted from persistent strong winds associated with increased ocean currents and coastal upwelling (Simpson, 1975; van der Hammen, 1974, 1982). Thus, it is possible to conclude that different species lineages of *Puya* evolved in response to various, often similar environmental pressures. Similar xeric adaptations displayed by these lineages probably illustrate convergent evolution.

RADIATION OF SPECIES IN RELATION TO ALTITUDE

Expansion of species lineages of *Puya* in the Andes was probably vertical as well as horizontal. The idea of vertical evolution has been postulated for several paramo taxa (Ericaceae, Melastomataceae, Rubiaceae; Chardon, 1938). Modern geographic distributions and phyletic alliances of various lineages of *Puya* suggest that only species confined to the punas (in Peru, Bolivia, and Argentina) could have evolved vertically (TABLE 7). Paramo species of *Puya* generally lack allies at lower elevations. These species radiated by a horizontal mechanism similar to some other paramo-dwelling groups (e.g., *Espeletia, Jamesonia, Diplostephium*; Cuatrecasas, 1957, 1979; A. C. Smith & Koch, 1935; Tryon, 1962).

DISJUNCTIONS

Vicariance and dispersal models explain the origin of disjunctions (Nelson & Platnick, 1981; Platnick & Nelson, 1978; Roe, 1967, 1972; Rosen, 1978; Whalen, 1983). There are apparently various degrees of disjunctions among the species of *Puya* (TABLE 5). Vicariance models postulate the appearance of barriers fragmenting the range of ancestral species. The congruence between the hypothesized cladistic relationships and the area of occurrence of species provides a useful indication of vicariance (see also Croizat *et al.*, 1974; Wiley, 1980, 1981). Such a congruence usually translates into parallel phylogenetic histories involving two or more lineages. Vicariance is a plausible mechanism especially for some high altitude lineages and putatively allied species pairs of *Puya* (TABLE 7). Replicate patterns of occurrences of sympatric groups and allied species pairs also suggest vicariance (TABLE 5).

Dispersal models, on the other hand, portray disjunction in light of dispersal across barriers, which is entirely dependent on unique dispersal abilities within the individual lineages rather than parallel patterns. For instance, the theory of long distance dispersal is compatible with the distribution of the *Puya tuberosa* complex across several intermountain valleys (FIGURE 2). Present evidence indicates that the disjunction of various species in this assemblage is probably an isolated event, not matched by any other subgroups in terms of parallel geographic patterns or cladistic relationships. Major disjunctions also occur as unique patterns in a few independent lineages (TABLE 5). These are undoubtedly an outcome of long distance dispersal.

PHENOLOGY AND GEOGRAPHIC DISTRIBUTION

Distinct phenological trends are correlated with some of the subclasses of geographic distributions of *Puya*. For example, phenological cycles synchronizing with climatic seasons are noted especially in the allopatric taxa (subclasses 1a and 1b). This trend may suggest a relatively long-term local stability of the species. When the range of a species expands over time, it may include environments differing from the parent one(s). This type of distributional change might induce specific (local) modifications in phenological traits. Thus, in species distributed widely across various macroclimates (e.g., species of subclass 1d), the relationship between phenology and the annual seasons is locally altered, revealing no apparent correlations. Phenology in sympatric taxa appears to be complex and remains as yet an intriguing, unexplored subject. To understand this complexity, we need data concerning socio-ecologic relationships, and the evolutionary histories of individual taxa as well as those of the habitats of sympatric species.

SUMMARY AND CONCLUSIONS

A majority of the species of *Puya* are allopatric and narrow endemics. They are most likely allopatrically derived and are isolated by geographic barriers. Speciation in many lineages primarily in the northern and central Andes and Chile resulted from episodes of aridity. Species appear to have colonized high altitudes directly from the differentiation of low elevation lineages as well as by a horizontal mechanism. Allied species became disjunct due to vicariance and dispersal events. Species extinctions probably occurred in a few lineages as a result of the obliteration of habitats brought about by localized arid periods and the uplift of tectonic plates. From Guayana, *Puya* immigrated into the Andes and attained its present range.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of my late Ph.D. advisor, Amy Jean Gilmartin. Her encouragement, support, discussion, and advice helped me in various aspects of bromeliad research. I also wish to acknowledge the support of the individuals who facilitated my field explorations in South America, particularly M. K. T. Arroyo, D. Diaz, T. Di Fulvio, A. Hunziker, R. Neumann,

L. Novara, F. Oliva, F. Ortega, J. Solomon, B. Stergios, and J. Steyermark. N. Platnick, P. F. Stevens, and J. Utley offered constructive comments on the earlier drafts of the manuscript. M. K. T. Arroyo, P. S. Ashton, and L. B. Smith are thanked for their useful discussions, and E. B. Schmidt and S. A. Spongberg gave helpful editorial advice. Also, I wish to extend special thanks to my wife, Usha, for her assistance in the field and herbarium and for typing the manuscript. The curators of GH, MO, NY, SEL, US, and WS are also acknowledged for permission to examine material in their herbaria and for sending specimens on loan. My field research was supported by a National Science Foundation doctoral dissertation improvement grant (BSR-8306999) and a National Geographic Society Research Grant (#3463-86).

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A RECONSIDERATION OF THE ACER PALMATUM COMPLEX IN CHINA, TAIWAN, AND KOREA

CHIN-SUNG CHANG[1]

Several varieties of *Acer palmatum* in China, Taiwan, and Korea are reevaluated based on morphology and flavonoid chemistry and a new taxonomic treatment is presented. The new name *Acer duplicatoserratum* var. *chinense* and new combinations for Taiwanese and Korean taxa are proposed. Distribution maps of *A. duplicatoserratum* and *A. duplicatoserratum* var. *chinense* are also presented.

During a comprehensive systematic study of *Acer* L., section *Palmata* Pax, series *Palmata,* nomenclatural problems were encountered in the *Acer palmatum* complex in China, Taiwan, and Korea. Data from morphology, geography, and flavonoid chemistry indicate that a new name is needed for the Chinese individuals of *A. palmatum* Thunberg. New combinations for the Taiwanese and Korean *Acer palmatum* are also required to clear up the taxonomic and nomenclatural confusion in this complex. Thirteen species of series *Palmata* (sensu de Jong, 1976) in central and eastern China, Taiwan, Korea, Japan, and western North America are currently recognized. Taxonomic treatment of the *Acer palmatum* complex in eastern Asia is further complicated by the existence of over 250 cultivars of *A. palmatum sensu lato,* developed and selected over more than 300 years (Vertrees, 1978). In Japan, Ogata (1965) recognized two taxa in this complex, *Acer palmatum* and *A. amoenum* Carrière, the latter with three varieties: *A. amoenum* var. *amoenum, A. amoenum* var. *nambuanum* (Koidz.) Ogata, and *A. amoenum* var. *matsumurae* (Koidz.) Ogata. Recent Japanese floras (Kitamura & Murata, 1984; Ohwi, 1984) simply treat *A. amoenum* as a variety or a subspecies of *A. palmatum,* although one of the former varieties of *A. amoenum,* subsp. *matsumurae* (Koidz.) Koidz., is still recognized as a distinct taxon. However, the name *A. palmatum* var. *matsumurae* (Koidz.) Makino is illegitimate since it was published as a *nomen nudum* (Ogata, 1965).

The *Acer palmatum* complex is widely distributed from Japan to Korea and to the coastal regions of the Yellow Sea and the East China Sea in continental China and in Taiwan (Ogata, 1965). The complex consists of the following taxa: *A. palmatum* var. *palmatum, A. palmatum* var. *amoenum* (Carrière) Ohwi, and *A. palmatum* subsp. *matsumurae* from Japan, the problematical *A. palmatum* var. *palmatum* from China, *A. duplicatoserratum* Hayata from Taiwan, and *A. palmatum* var. *pilosum* Nakai from Korea.

The purpose of this study was to reevaluate the taxonomic status of the taxa

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Journal of the Arnold Arboretum **71**: 553–565. October, 1990.

in this complex using morphological, flavonoid, and field data. In particular, flavonoid data had already been applied with considerable success to systematic problems in *Acer* by Delendick (1981, 1984, 1985).

MATERIALS AND METHODS

More than 50 individuals of the *Acer palmatum* complex and *A. pseudosieboldianum* (Pax) Komarov were collected from natural populations in Korea, Japan, and Taiwan (only two individuals) mainly during the summers of 1986, 1987 and 1988 (see Appendix). Taxa of more limited distribution in mainland China were examined, with permission, using herbarium specimens from A, GH, KYO, PE, NF, TAI, TI, and TUS.

The extraction of foliar flavonoids followed the methods of Mabry and colleagues (1970) and Giannasi (1975). The flavonoid survey employed two-dimensional paper chromatography using Whatmann 3 MM paper. The solvents used were TBA (tertiary butanol : acetic acid : water, 3:1:1, v/v) as the first solvent and 15% HOAc (acetic acid : water, 15:85, v/v) as the second solvent. The flavonoid profiles were viewed under UV light and colors were recorded before and after fuming with ammonia vapor. Comparisons of the spectral and Rf data were made with published data (Delendick, 1981; Mabry *et al.*, 1970). Structural identification of the flavonoids was accomplished using UV spectroscopy and enzymatic and acid hydrolysis (trifluoroacetic acid) for sugar analysis (Wilkins & Bohm, 1976). Recovered sugars were cochromatographed with standard sugars in one-dimension using ethyl acetate : pyridine : water (5:1.6:1, v/v) as the solvent. The sugars were visualized by spraying with p-anisidine hydrochloric acid (Pridham, 1956).

RESULTS AND DISCUSSION

Taiwanese Acer palmatum

The Taiwanese member of the *Acer palmatum* complex was named *A. duplicatoserratum* by Hayata (1911) and was thought to be endemic to Taiwan (Formosa). Hayata used a Konishi specimen (collected in June, 1902) as the type specimen of *A. duplicatoserratum.* Koidzumi (1911) treated this taxon as a variety of *A. palmatum,* while Nemoto (1936) regarded it as a variety of *A. ornatum* Carrière. Sasaki (1928) described the taxon as *A. matsumurae* var. *formosum* Sasaki but did so without a description or reference, thereby creating an illegitimate *nomen nudum* (Li, 1952). Since the name *A. ornatum* had already been applied to one of the cultivated forms of *A. palmatum* var. *amoenum* (Hara, 1954; Ogata, 1965) by Carrière (1867), Nemoto's *A. ornatum* var. *matsumurae β. spontaneum* subvar. *formosanum* (Koidz.) Nemoto was illegitimate. Li (1952) renamed it *A. palmatum* var. *pubescens* and characterized it as having five-lobed leaves and pubescent young branches, inflorescences, mature leaves, and petioles. He cited *Suzuki 17859* (PE) as the holotype. Fang (1981) agreed with Hayata's concept concerning the status of this taxon and thus treated it

as a distinct species, *A. duplicatoserratum.* Despite these discernible differences, most Taiwanese botanists (Liu, 1962; Lu & Liao, 1988) follow Li's treatment and use the name *A. palmatum* var. *pubescens* for *A. duplicatoserratum.*

Indeed, pubescence on the ovary, mature leaves, and petioles of the Taiwanese taxon distinguishes it from its putatively related Japanese and Korean varieties of *Acer palmatum.* Pubescence is present on another distantly related Japanese endemic, *A. sieboldianum* Miguel, but the 9- to 11-lobed leaves of *A. sieboldianum* easily distinguish it from the Taiwanese taxon, which has 5- to 7-lobed leaves (TABLE 1).

The flavonoid complement of the Taiwanese taxon (*Acer duplicatoserratum* in TABLE 2) is quite distinct in comparison to Japanese and Korean *A. palmatum* var. *palmatum* and *A. palmatum* var. *amoenum* due to the absence of flavones and glycoflavones (see TABLE 2, compounds 11–16) characteristically found in the Japanese taxa. Delendick's (1981) extensive flavonoid survey of *Acer* documented two chemical types within section *Palmata.* The "*palmatum*" type dominated by the O- and C-glycosylflavones, and the "*japonicum*" type dominated by flavonol-O-glycosides (TABLE 2, compounds 1–10), but with C-glycosylflavones absent. As shown in TABLE 2, the Taiwanese *A. duplicatoserratum* clearly belongs to the "*japonicum*" type, and not the "*palmatum*" type as suggested by previous morphological studies alone.

Since the Taiwanese taxon is distinct morphologically, chemically and geographically, it is treated as a distinct species, *Acer duplicatoserratum,* rather than as a variety of *A. palmatum.*

Acer duplicatoserratum Hayata, J. Coll. Sci. Imp. Univ. Tokyo **30:** 65. 1911. TYPE: Taiwan. Taitung Hsien, Mataianchi, *N. Konishi s.n.,* June 1902. (Photograph of holotype, TI!).

Acer palmatum Thunb. subsp. *matsumurae* Koidz. var. *spontaneum* Koidz. subvar. *formosanum* Koidz., J. Coll. Sci. Imp. Univ. Tokyo **32:** 50. 1911. TYPE: *Konishi s.n.,* June, 1902. (TI, as photograph!).

Acer matsumurae Koidz. var. *formosanum* Sasaki, List of Plants of Formosa p. 324. 1928, *nomen nudum.*

Acer ornatum Carr. var. *matsumurae* Koidz. *β. spontaneum* (Koidz.) Nemoto subvar. *formosanum* (Koidz.) Nemoto, Flora of Japan, Supplement p. 454. 1936. TYPE: *Konishi s.n.,* June, 1902. (TI, as photograph!).

Acer palmatum Thunb. var. *pubescens* Li, Pacific Sci. **6:** 293. 1952. TYPE: *Sasaki 17859* (A!, PE!).

Acer *palmatum* subsp. *pubescens* (Li) E. Murray, Kalmia **8**(2–3): 20. 1978. TYPE: *Sasaki 17859* (A!, PE!).

SPECIMENS EXAMINED: **Taiwan.** HUALIEN HSIEN: *Huang 166* (TAI, TUS), *Liu & Liu 135* (TAI), *Sasaki 9478* (TAI), *Tang 084* (TAI). ILAN HSIEN: *Sasaki s.n.* (A; Herb. no. 071527, TAI), *Hibino et al. s.n.* (Herb. no. 082788, TAI). NANTOW HSIEN: *Chang 1374, Chang 1376* (GA), *Kuo 14642* (GA). TAICHUNG HSIEN: *Tang 437* (TAI), *Ohwi s.n.* (KYO). TAIPEI HSIEN: *Suzuki 17859* (A, PE), *Suzuki 16490* (PE), *Ohwi s.n.* (KYO).

DISTRIBUTION: endemic to north and central Taiwan (MAP 1); distributed very locally in deciduous forests at altitudes of 1000–2000 m.

TABLE 1. **Morphological comparison of the Acer palmatum complex and related taxa.**[a]

TAXA	NUMBER OF LEAF LOBES	LEAF WIDTH (cm)	NUTLET LENGTH (mm)	WING LENGTH (cm)	OVARY PUBESCENCE	PETIOLE PUBESCENCE
A. duplicatoserratum var. *duplicatoserratum*	7	4.9–7.1 (6.0)	2.5–5.0 (3.4)	1.3–2.0 (1.7)	+	+
A. duplicatoserratum var. *chinense*	5–9 (6.6)	4.8–8.1 (6.2)	4.0–5.0 (4.5)	1.7–2.3 (2.0)	+	–
A. ceriferum	5–7 (6)	4.4–5.0 (4.7)	4.0	2.0–2.1 (2.05)	?	+
A. sieboldianum	9	5.8–9.1 (6.5)	2.5–5.0 (3.95)	1.4–2.4 (1.9)	+	+
A. pseudosieboldianum	9–11 (9.4)	7.5–10.3 (8.8)	3.0–5.5 (4.1)	1.4–2.4 (1.9)	+	+
A. pubipalmatum	5	5.3–6.7 (5.7)	3.0	1.7–1.8 (1.75)	+	+
A. palmatum var. *palmatum*	5–7 (6.6)	4.0–7.8 (6.1)	3.0	1.3–1.6 (1.4)	–	–
A. palmatum var. *amoenum*	5–9 (7.0)	6.0–10.0 (8.5)	3.0–5.5 (4.3)	1.6–2.3 (2.0)	–	–

[a] Range of variation with mean values in parentheses.

Chinese Acer palmatum

Fang (1932a, 1932b, 1939, 1981) recognized two varieties of *Acer palmatum* in China, viz. var. *thunbergii* Pax and var. *palmatum*. The type specimen of *A. palmatum* consists of two different collections mounted on the same sheet. They are currently recognized as two different taxa, *A. palmatum* var. *amoenum* and var. *palmatum*. However, Pax (1886) applied a single name, *A. palmatum* var. *thunbergii*, to Thunberg's type specimen. Since *A. palmatum* var. *thunbergii* was applied to two different taxa, it was later rejected as an illegitimate name by Hara (1954) and Ogata (1965). Fang (1932a), apparently unaware of his error, nonetheless applied the illegitimate name var. *thunbergii* to specimens with deeply lobed leaves. He included not only the native Chinese plants under var. *palmatum* and var. *thunbergii* but also included many cultivated plants in China (probably introduced from Japan), which clearly belong to the two currently recognized Japanese taxa, var. *palmatum* and var. *amoenum*. Fang's (1932a) description of Chinese var. *palmatum* is further contradictory to concepts of the Japanese and Korean var. *palmatum* (Koidzumi, 1925; Nakai, 1932; Hara, 1954; Lee, 1979). For example, Fang described Chinese var. *palmatum* as having globose nutlets 7 mm in diameter, wings 2–2.5 cm long and 1 cm broad (real measurements indicate that nutlets are 4.5 mm in diameter, wings 1.7–2.3 cm; see Table 1). In fact, Japanese and Korean var. *palmatum* have slender nutlets 3 mm in diameter, with wings 1.4 cm long (see Table 1 and Figure). In addition, the ovaries of the Japanese and Korean individuals of var. *palmatum* are distinctly glabrous, unlike Fang's Chinese individuals of var. *palmatum*, which have densely villous ovaries (see Figure). The fruit shape and size of Chinese var. *palmatum* are more like those of var. *amoenum*. However, the leaves of var. *amoenum* (6–10 cm in diameter; based on measurements of over 50 specimens) are larger than those of Chinese var. *palmatum* (4.8–8.1 cm, Table 1 as *A. duplicatoserratum* var. *chinense*; based on measurements of 14 specimens).

This Chinese taxon like the Taiwanese *Acer duplicatoserratum* belongs to the typical "*japonicum*" flavonoid type, i.e., no O- and C-glycosylflavone (see Table 2). However, the Chinese *A. palmatum* var. *palmatum* sensu Fang (now recognized as *A. duplicatoserratum* var. *chinense* in Table 2) is distinguished chemically from Taiwanese *A. duplicatoserratum* var. *duplicatoserratum* by the presence of two kaempferol 3-O-glycosides and myricetin 3-O-rhamnoside (compound 10). These compounds are absent in typical Taiwanese *A. duplicatoserratum* var. *duplicatoserratum* (Table 2). It is obvious that while distinct, these two taxa are closely related. The main difference between them is that *A. duplicatoserratum* has very pubescent leaves and petioles, while the Chinese taxon lacks pubescence on mature leaves. This is now reflected in being accorded only varietal status. Based on these chemical and morphological data, however, it appears that the Chinese taxon is more appropriately treated as a variety of *A. duplicatoserratum* rather than as a variety of *A. palmatum*.

Acer duplicatoserratum Hayata var. **chinense** C. S. Chang, var. nov. Figure.

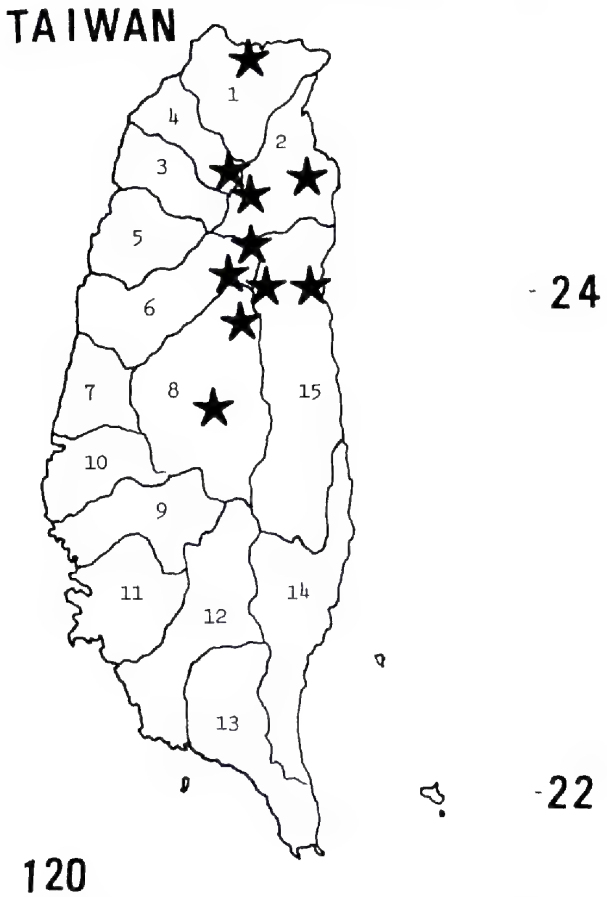
Acer palmatum var. *palmatum* auct. non Thunb.; Fang, Contr. Biol. Lab. Chin. Assoc. Advacem. Sci., Sect. Bot. **8:** 163, 164. 1932.

TABLE 2. **Flavonoid chemistry of the Acer palmatum complex and related taxa.**

	FLAVONOL										FLAVONES						UNKNOWN		
	K				Q					M	L–O	A–C			L–C				
	1[a]	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Japonicum type																			
A. palmatum var. *pilosum*		X	X		X	X	X	X	X								X	X	X
A. pseudosieboldianum		X	X		X	X	X	X	X								X	X	X
A. duplicatoserratum var. *duplicatoserratum*					X	(X)[b]	X	(X)	X									X	X
A. duplicatoserratum var. *chinense*	X	X			(X)	X	X	X	X	X								X	X
A. pubipalmatum	X	X			X	X	X		X									X	X
A. ceriferum	X	X			X	X	X	X	X	X								X	X
Palmatum type																			
A. palmatum var. *palmatum*		(X)	(X)	(X)	(X)		(X)	(X)	X		X	X	X	(X)	X	X		X	X
A. palmatum var. *amoenum*			(X)		(X)				X		X	X	X	X	X	X		X	X

[a] Key: K = kaempferol; Q = quercetin; M = myricetin; L–O = luteolin O-glycoside; A–C = apigenin C-glycoside; L–C = luteolin C-glycoside. Specific compounds: 1, K 3-O-rhamnoside; 2, K 3-O-xyloside; 3, K 3-O-arabinoside; 4, K 3-O-xylose-rhamnose; 5, Q 3-O-glucoside; 6, Q 3-O-xyloside; 7, Q 3-O-rhamnoside; 8, Q 3-O-glucose-xylose; 9, Q 3-O-glucose-rhamnose; 10, M 3-O-rhamnoside; 11, L 7-O-glucoside; 12, A 6-C-glycoside; 13, A 8-C-glycoside; 14, A 6,8-di-C-glycoside; 15, L 6-C-glycoside; 16, L 8-C-glycoside; 17, unknown; 18, unknown; 19, ellagic acid.

[b] (X) compound detected in trace quantities only and of sporadic occurrence.



MAP 1. Distribution of *Acer duplicatoserratum* Hayata in Taiwan.

Ramuli glabri; folia ambitu orbicularia 6.5–7.5 cm diametro, palmatim 7–9-loba, lobis lanceolatis, acuminatis, argute et dupliciter serratis, 4.5–5 cm longa, petiolis 4–5 cm longis; flores 3–4 mm diametro purpurei 2 mm longi; ovarium dense et longe lanatum; samarae loculo globoso 5 mm diametro glabro, incluso 2.2 cm longae, 8 mm latae, alis angulo obtuso divergent.

TYPE: **China.** ANHUI PROVINCE: Mt. Chang-gon-shan, Wu-yuan, alt. ca. 2500 ft (ca. 820 m), a big shrub (30 ft, ca. 10 m), DBH 10" (25 cm), common in wood along the stream, *R. C. Ching 3243,* August 17, 1925 (holotype, A).

ADDITIONAL SPECIMENS EXAMINED: **China.** ANHUI PROVINCE: Mt. Chu-hwa-shan, *Ching 2828* (A), Mt. Hwang-shan, *Liou & Tsoong 2931* (PE). HUNAN PROVINCE: Mt. Mo-fou-shan (Mu-fu-shan), *Hsiung 5824* (GH). JIANGXI PROVINCE: Mt. Lu-shan, *Hu 2414* (A, NAS), *Ip 1784* (A), Kuling, *Wilson 1504* (A, US), *Wilson 1505* (A). ZHEJIANG PROVINCE: Tien-mu-shan *Fang 21261* (PE), Tien-tai-shan, *Ching 1515* (A), *Ching 1417* (A, GH), *Chiao 14317* (A, PE), *Chiao 14379* (A, US), *Song 674* (NAS), Chang-huwa, *Hu 22768* (NAS).

DISTRIBUTION: endemic to eastern China (MAP 2); distributed in deciduous forests at altitudes of 800–1500 m.

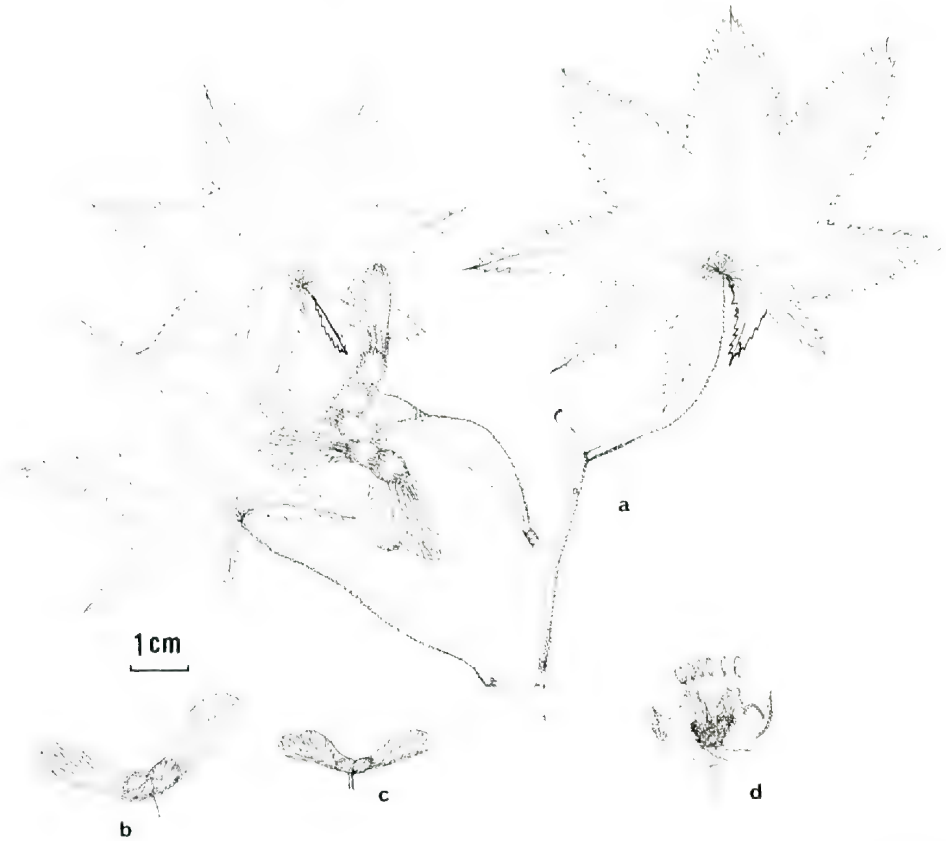
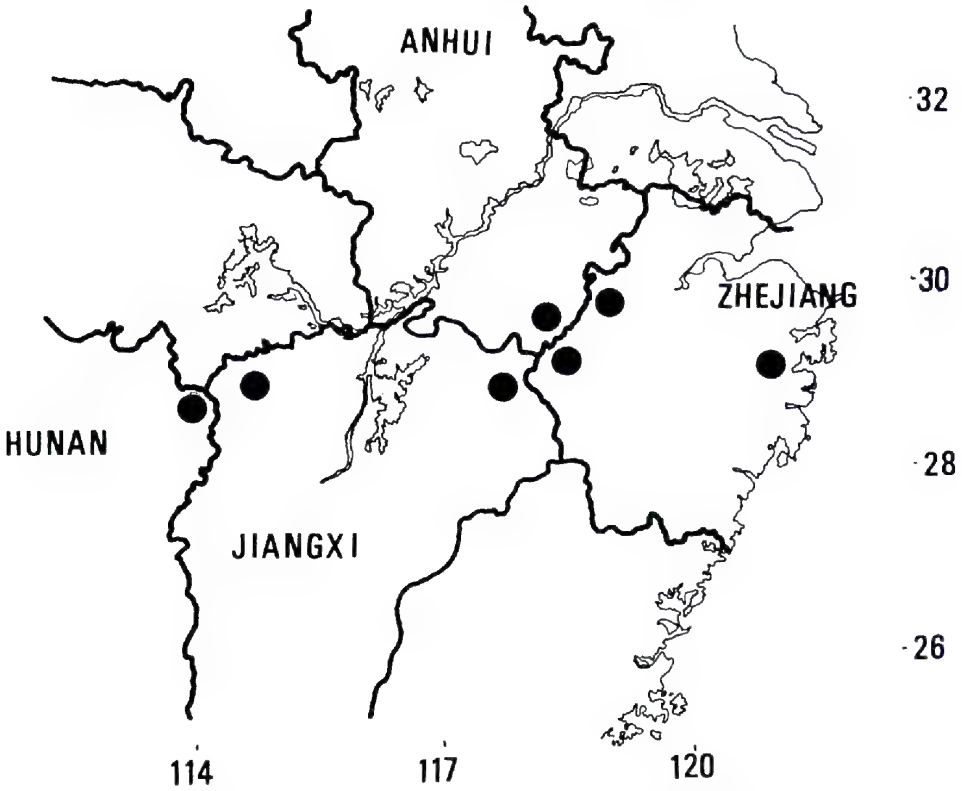


FIGURE. *Acer duplicatoserratum* var. *chinense*: a, habit of branchlet with fruit (based on *Ching 3243*); b, fruit (based on *Ching 3243*); c, fruit of *A. palmatum* for comparison (based on *Chang 1018*); d, flower of *A. duplicatoserratum* var. *chinense* (based on *Ching 1515*).

Acer pubipalmatum Fang, which is also known primarily from Zhejiang Province, is closely related to *A. duplicatoserratum* var. *chinense*. Their close relationship is reflected by their similar flavonoid complements (TABLE 2) as well as by their similar morphology. However, *A. pubipalmatum* has smaller fruits, very deeply five-lobed leaves, villous hairs on the leaf veins and petioles, and densely pubescent ovaries and sepals.

Morphologically, the Chinese *Acer ceriferum* Rehder (Rehder, 1911), which has thus far been found only in western Hubei Province (*Wilson 1934*), appears to be closely related to the Taiwanese *A. duplicatoserratum* var. *duplicatoserratum*. The morphological differences between these two taxa are mainly in the degree of pubescence on leaves and twigs (TABLE 1). However, the flavonoid chemistry indicates that *A. ceriferum* is most closely related to *A. duplicatoserratum* var. *chinense* rather than var. *duplicatoserratum* because of the presence of myricetin 3-O-rhamnoside. These relationships are certainly logical from a phytogeographical standpoint since both *A. duplicatoserratum* var. *chinense* and *A. ceriferum* are mainland Chinese taxa (see below). A difference in flower color is a significant distinguishing character that separates *A. pseudo-*



MAP 2. Distribution of *Acer duplicatoserratum* var. *chinense* C. S. Chang in eastern China.

sieboldianum and *A. sieboldianum* (see KEY). Because flower color of *A. ceriferum* and members of the *A. duplicatoserratum* complex is unknown, nomenclatural changes involving *A. ceriferum* await further study.

KOREAN ACER PALMATUM

Several varieties of *Acer palmatum* have been described from Korea, although some have not been accepted. For example, the name *A. palmatum* var. *coreanum* Nakai (Nakai, 1914) was rejected by Ogata (1965) based on Article 71 of the *International Code of Botanical Nomenclature* (Lanjouw, 1961) since this name was applied to an abnormal form that lacked petals in female flowers. This Article, however, was deleted from the *Code* at the Leningrad Congress in 1985 (Greuter, 1988). Nakai (1919) characterized *A. palmatum* var. *pilosum* Nakai as having leaves with 7 to 9 lobes, doubly serrate margins, and pedicels and peduncles densely covered with white hairs. This variety, along with *A. palmatum* var. *palmatum,* is still listed in the Korean flora (Lee, 1979). The known localities for *A. palmatum* var. *pilosum* include Un-san City in Pyong-an-buk-do Province (*Wilson 8649,* A, TI), Kyong-sung-gun, Nam-ha-dan in Ham-kyong-buk-do Province (*Nakai 7235,* TI) and Mt. Chil-bo-san in Ham-kyong-buk-do Province in North Korea (*Nakai 7236,* TI).

Flavonoid data (TABLE 2), however, clearly indicate that this taxon is chemically identical to *A. pseudosieboldianum* rather than *A. palmatum* var. *palmatum* (*sensu lato*), which also occurs in southeastern Korea. It appears that this taxon is merely an extremely small-leaved and small-fruited form of *A. pseudosieboldianum* erroneously identified as a variety of *A. palmatum.* It is therefore proposed that *A. palmatum* var. *pilosum* be treated as conspecific with *A. pseudosieboldianum,* which is common in the Korean peninsula and northeastern China. Synonymy for *A. pseudosieboldianum* is presented below.

Acer pseudosieboldianum (Pax) Komarov, Trudy Glavn. Bot. Sada **22:** 725. 1904. TYPE: China. Northeast (Manchuria) Port Bruce, *Maximowicz s.n.,* 1860 (syntype, NY).

Acer circumlobatum var. *pseudosieboldianum* Pax, Bot. Jahrb. Syst. **7:** 199. 1886.

Acer sieboldianum var. *mandshuricum* Maxim., Mélanges Biol. Bull. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg **12:** 433. 1886. TYPE: not seen.

Acer palmatum var. *pilosum* Nakai, Bot. Mag. Tokyo **33:** 59. 1919. TYPE: Korea, Pyong-an-buk-do Province, *Wilson 8649* (lectotype, here chosen, A; isolectotype, TI).

DISTRIBUTION AND KEY TO THE ACER PALMATUM COMPLEX AND RELATED TAXA

It appears that *Acer palmatum* var. *palmatum* (*sensu stricto*) is restricted to southwestern Korea (Cheol-la-nam-do, Cheol-la-buk-do, and Je-ju-do Provinces) and Japan on Honshu (Fukushima to Yamaguchi Prefectures), Shikoku, and Kyushu. The related *A. palmatum* var. *amoenum,* however, is common in Japan from Hokkaido to Kyushu (Ogata, 1965). The other taxa of the complex—*A. duplicatoserratum* var. *duplicatoserratum, A. duplicatoserratum* var. *chinense* and *A. pseudosieboldianum*—that are often linked to *A. palmatum* appear, in fact, to be distinct and/or with close ties to other sympatric taxa in China, Korea or Taiwan. The flavonoid data have been especially helpful in delimiting inter- and intraspecific relationships.

The following key is provided to aid in the identification of individuals in the *Acer palmatum* complex and related taxa in eastern Asia. Most of the taxa can be separated based on vegetative characters. However, without reproductive characters, it is extremely difficult to distinguish between *A. sieboldianum* and *A. pseudosieboldianum* and between *A. palmatum* var. *amoenum* and *A. duplicatoserratum* var. *chinense* (TABLE 1). Nonetheless, knowledge of geographical distribution, in addition to floral and other morphological characters, can be effectively employed for the identification of the taxa.

KEY TO THE ACER PALMATUM COMPLEX AND RELATED TAXA

1. Ovary glabrous; petioles and peduncles glabrous or nearly so.
   2. Nutlet of fruit ca. 2.5 mm wide and ca. 3 mm long; wings of fruits ca. 6 mm wide and ca. 14 mm long; leaf blades 4–7 cm wide; plants of southwestern Korea and Japan. ..... *A. palmatum* var. *palmatum.*

2. Nutlet of fruits ca. 4 mm wide and ca. 4.5 mm long; wings of fruits ca. 8 mm wide and ca. 20 mm long; leaf blades 6–10 cm wide; plants from Japan. ..... *A. palmatum* var. *amoenum.*

1. Ovary villous; petioles and peduncles pubescent at least when young.
   3. Leaf blades 9–11-lobed; margins deeply serrated with teeth ca. 2–3 mm long.
      4. Flowers yellow; leaf blade pubescent; petioles hairy; plants of Japan. ..... *A. sieboldianum.*
      4. Flowers purple; leaf blade pubescent only on veins; petioles very hairy; plants of Korea, northeastern China, and southern Siberia. ..... *A. pseudosieboldianum.*
   3. Leaf blades 5–7-lobed (rarely 9-lobed); margins with teeth less than 1 mm long.
      5. Leaf blades mostly deeply 5-lobed; nutlet of fruit small (ca. 3 mm); plants of eastern China. ..... *A. pubipalmatum.*
      5. Leaf blades mostly 7-lobed (rarely 9-lobed); nutlet of fruit large (ca. 3.4–4.5 mm).
         6. Petioles of mature leaves persistently pubescent; plants of Taiwan. ..... *A. duplicatoserratum* var. *duplicatoserratum.*
         6. Petioles of young leaves pubescent, becoming glabrous with age; plants of eastern China. ..... *A. duplicatoserratum* var. *chinense.*

ACKNOWLEDGMENTS

I would like to express my appreciation to David E. Giannasi for his support and guidance. I also gratefully acknowledge the assistance of the following people: Samuel B. Jones, David E. Boufford, Nancy Coile, Hiroyoshi Ohashi, Mike Moore, Derek Focho, Chen-Meng Kuo, Tzen-Yuh Chiang (for field work in Taiwan), Jin Murata (for photographs of type specimens), Rupert Barneby (for correcting the Latin description), and Tchang-Bok Lee (for helpful discussions of Korean taxa). I would also like to thank T. Delendick and J. Gurevitch for their critical reviews of the manuscript. I am gratefully indebted to the directors and the curators of the following herbaria for the loan of specimens: A, GH, KYO, NF, PE, TAI, TI, and TUS. This study was supported by four Student Research Grants from the Botany Department, University of Georgia.

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APPENDIX. **Material used for chemical survey.**

Acer duplicatoserratum Hayata: **Taiwan.** NANTOW HSIEN: *Chang 1376, Chang 1374, Kuo 14642*; TAIPEI HSIEN: *Ohwi s.n.* (KYO); HUALIEN HSIEN: *Huang 166* (TUS), *Liu & Liu 135* (TAI), *Tang 84* (TAI); TAICHUNG HSIEN: *Ohwi s.n.* (KYO), *Tang 437* (TAI); ILAN HSIEN: *Hibino et al. s.n.* (Herb. no. 082788, TAI).

Acer duplicatoserratum Hayata var. *chinense* C. S. Chang: **China.** ZHEJIANG PROVINCE: *Ching 1417* (A), *Chiao 14379* (US); ANHUI PROVINCE: *Ching 3243* (A), *Liou & Tsuong 2931* (PE); JIANGXI PROVINCE: *Hu 2414* (NAS).

Acer pseudosieboldianum (Pax) Komarov (as *A. palmatum* var. *pilosum* Nakai): **Korea.** HAM-KYONG-BUK-DO PROVINCE: *Nakai 7235* (TI); PYONG-AN-NAM-DO PROVINCE: *Wilson 8649* (TI).

Acer pubipalmatum Fang: **China.** ZHEJIANG PROVINCE: *Chen 493* (PE).

BEGONIA AUSTROTAIWANENSIS (BEGONIACEAE), A NEW SPECIES FROM SOUTHERN TAIWAN

CHING-I PENG[1] AND YUNG-KUAN CHEN[1]

A new species of *Begonia, B. austrotaiwanensis* Chen & Peng from southern Taiwan, is described and illustrated. This species is usually found on moist, steep, rocky slopes at 200–800 m alt. Diagnostic features include an acaulescent, deciduous habit; moniliform rhizomes consisting of several ellipsoid to subglobose units with persistent stipules; inflorescences arising directly from the rhizome; flowers of both sexes scented, the staminate ones with four tepals, the pistillate ones with three tepals and two styles; two-locular ovaries; axile placentation; unequally three-winged capsules, with the abaxial wing narrowly triangular, erect, and much protruded; and a chromosome number of $n = 18$. The systematic position of *B. austrotaiwanensis* is in the Asiatic section *Platycentrum.*

During the past decade three new species of *Begonia* have been added to the flora of Taiwan (T. S. Liu & Lai, 1977; Y.-C. Liu & Ou, 1982; Peng *et al.,* 1988). Most recently, Ying (1988) proposed *Begonia fenchihuensis* as new; however, an examination of his original description and type specimens reveals that it is synonymous with *B. buimontana,* published about half a century ago by Yamamoto (1933). Nine species of *Begonia,* five of them endemic, are presently known from Taiwan. In our systematic revision of the Taiwanese species of *Begonia,* we discovered a distinct new species that brings the total to ten; it is described here.

Begonia austrotaiwanensis Y.-K. Chen & C.-I Peng, sp. nov. FIGURE 1.

Herba acaulis rhizomatibus reptantibus praedita, rhizomate aspectu grosse moniliforme, stipulis persistentibus triangularibus, 7–22 mm longis, 4–9 mm latis, induto. Folia oblique ovata, ad 38 cm longa, 32 cm lata. Inflorescentiae ad 55 cm longae, axillares ex rhizomate statim orientes. Flores omnes rosei, fragrantes. Flos ♂: tepala 4, decussata, duobus exterioribus rotundis ad orbiculares, 13–35 mm longis, 9–32 mm latis. Flos ♀: tepala 3, 2-seriatim disposita, duobus exterioribus oppositis, rotundis ad oblata, 16–32 mm longis, 7–23 mm latis, uno interiore oblanceolato ad obovato, 12–23 mm longo, 7–23 mm lato; styli 2. Fructus capsulares, inaequaliter alato, corpore ellipsoideo, ca. 15 mm longo, 7–8 mm in diametro, ala abaxiali recta, conspicue producta, anguste triangulari, 27–46 mm longa, 9–15 mm lata, alis lateralibus multo angustioribus, 9–14 mm longis, 2.3–3.5 mm latis. Numerus chromosomatum, $n = 18$.

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Journal of the Arnold Arboretum **71:** 567–574. October, 1990.

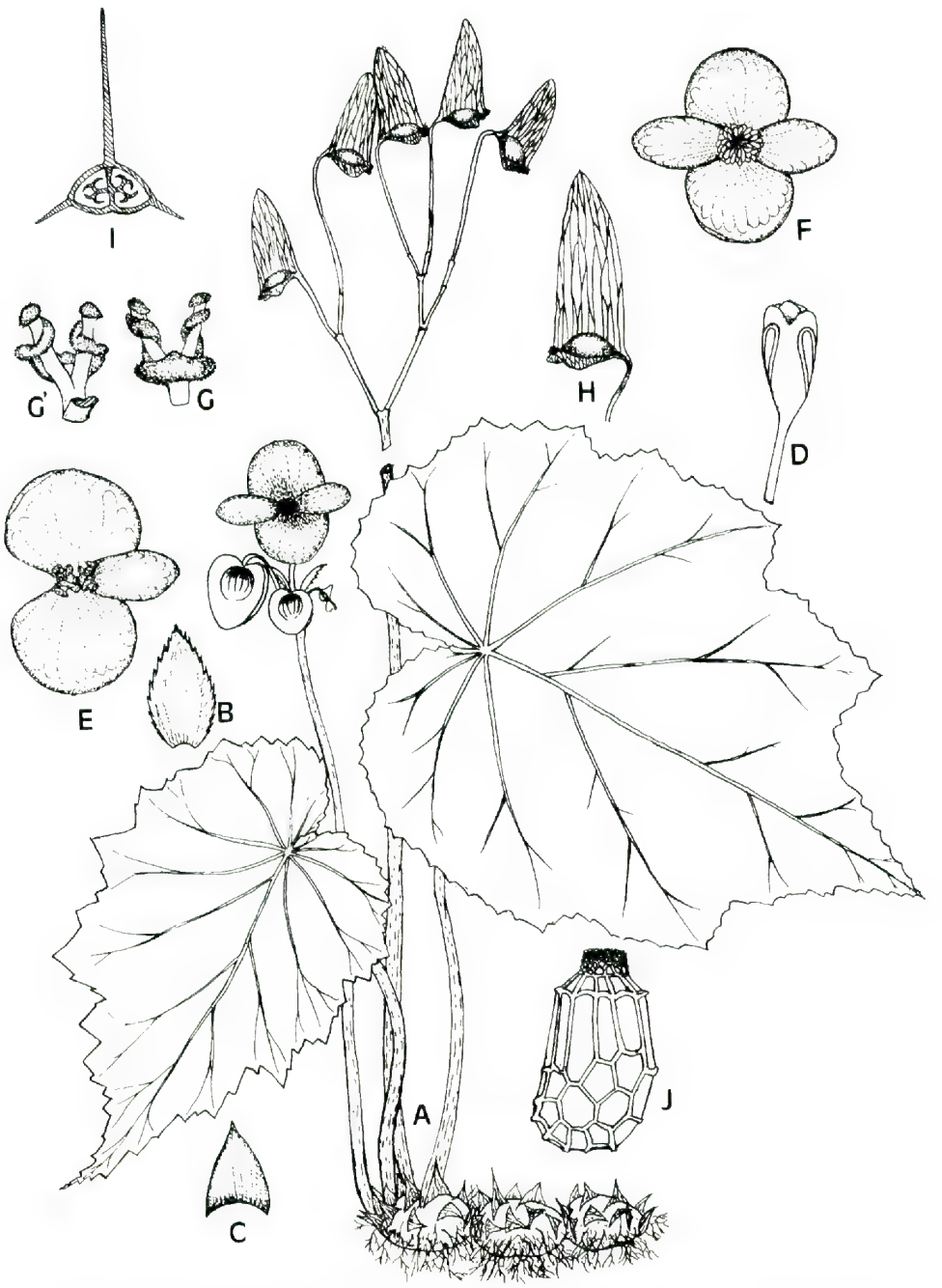


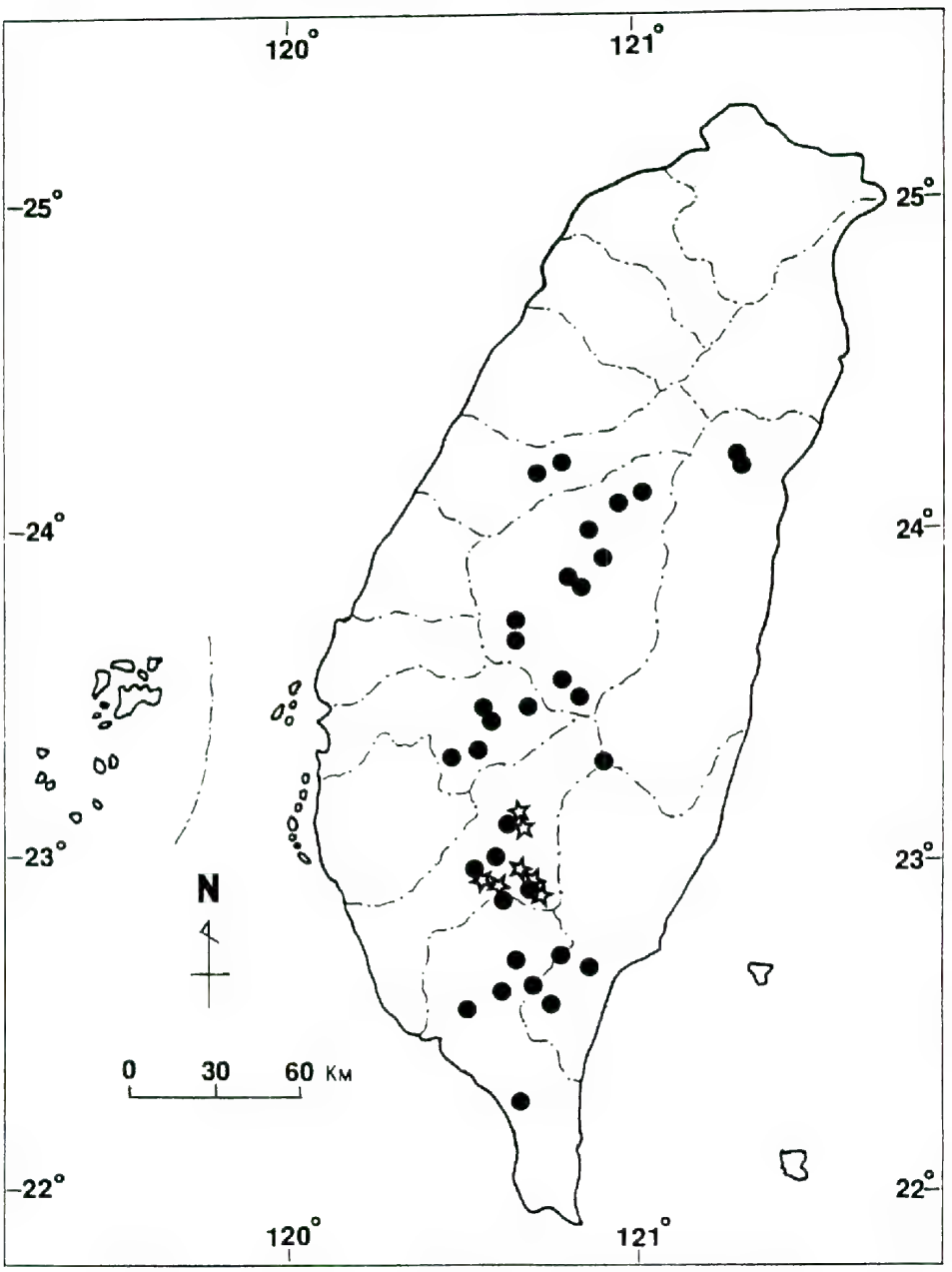
FIGURE 1. *Begonia austrotaiwanensis*: A, habit, × 0.3; B, bract, × 1.2; C, stipule, × 0.6; D, stamen, × 6; E, pistillate flower, × 0.6; F, staminate flower, × 0.6; G, G', style, × 3; H, fruit, × 0.6; I, fruit, cross section, showing placentation, × 0.9; J, seed, × 60. (A–I from *Chen 100*, J from *Chen 522*.)

Perennial, deciduous, acaulescent herb with creeping rhizome; rhizome moniliform, consisting of several ellipsoid to subglobose units each 9–50 mm long, 7–25 mm in diameter, densely covered by persistent stipules, these triangular, 7–22 mm long, 4–9 mm wide, acuminate at apex. Leaves with petiole to 40 cm long, 9 mm in diameter, greenish or sometimes reddish; blade obliquely to broadly ovate, 13–38 by 10–32 cm, acuminate to cuspidate at apex, unequally cordate at base (often lobed in adult leaves), irregularly dentate-serrate, green, sometimes with white foveolate spots on upper surface and/or broad brown belts along adaxial veins, chartaceous to slightly succulent, venation palmate, the veins 6 to 10. Bracts caducous, in pairs, narrowly ovate to elliptic, 8–12 by 3.5–6.5 mm, acute at apex, serrate, pale green, papery to nearly succulent, glabrous. Inflorescences in androgynous dichasial cymes to 55 cm long arising directly from rhizome; peduncle erect, to 42 cm long, 8 mm in diameter. Flowers of both sexes pinkish, scented. Staminate flowers with tepals 4, decussate, spreading, margin sometimes reflexed, the outer 2 rotund to orbicular, 13–35 by 9–32 mm, the inner 2 oblanceolate to narrowly obovate, 10–32 by 6–18 mm; stamens 51 to 66, golf club shaped, yellow, the filaments free, 0.9–2.7 mm long, the anthers 1.8–2.3 mm long, 0.8–1.2 mm in diameter. Pistillate flowers with tepals 3 (very rarely 2 or 4, the fourth much reduced when present), the outer 2 opposite, rotund to oblate, 16–32 by 14–37 mm, the inner 1 oblanceolate to obovate, 12–23 by 7–23 mm; styles 2, Y-shaped, 4.2–5.3 mm long, yellow, the base separate to short-connate, 2.1–2.6 mm long, each arm covered with a spiral, papillose stigmatic band; ovary 2-locular, unequally 3-winged, obovoid, white to pale green, glabrous; placentae axile, bilamellate, the lamella forked. Infructescences to 72 cm long, the fruit-bearing pedicels 28–47 mm long; mature fruit a dry, trigonous, very unequally 3-winged capsule, the body ellipsoid, 9–15 mm long, 7–8 mm in diameter, the abaxial wing erect, much protruded, narrowly triangular, 27–46 by 9–15 mm, the lateral wings much narrower, 2.3–3.5 by 9–14 mm. Seeds numerous, narrowly ovoid, 0.39–0.43 mm long, 0.19–0.25 mm in diameter, rounded at apex, constricted at micropylar end, yellowish brown. Chromosome number, $n = 18$.

DISTRIBUTION. Presently known only from Kaohsiung Hsien, Taiwan (see MAP 1), 200–1000 m alt.

TYPE: Taiwan, Kaohsiung Hsien, Mawlin District, Shanping, 22°58′N, 120°41′E, elev. ca. 700 m, on moist, steep, rocky slope, *Y.-K. Chen 100* (living collection made on 27 July, 1987; type specimens pressed from cultivated plants in October 1988) (holotype, HAST; isotypes, GH, K, MO, NY, TAI, TAIF, US).

ADDITIONAL SPECIMENS EXAMINED. **Taiwan.** KAOHSIUNG HSIEN. Maolin Distr.: Shanping, 22°58′N, 120°41′E, elev. ca. 700 m, *Chen 522* (HAST), *Peng 10091* (HAST); Shanping logging trail, 22°58′N, 120°40′E, elev. ca. 600 m, *Chen 354* (HAST); Tona Hot Spring, 22°55′N, 120°42′E, elev. ca. 350 m, *Chen 638* (HAST); Tona logging trail, 22°54′N, 120°43′E, elev. ca. 750 m, *Chen & Peng 375* (HAST), 22°53′N, 120°44′E, elev. ca. 800 m, *Chen & Peng 381* (HAST); Tachin Waterfall, 22°52′N, 120°39′E, elev. ca. 300 m, *Chen 619* (HAST). Liukuei Distr.: Wangshanchiao, 22°55′N, 120°38′E, elev. ca. 200 m, *Chen 344* (HAST).



MAP 1. Distribution of *Begonia austrotaiwanensis* (stars) and *B. laciniata* (dots) in Taiwan.

HABITAT AND ASSOCIATED PLANTS. *Begonia austrotaiwanensis* often grows in moist, shallow soil on steep, rocky slopes and in somewhat shady habitats. The following species are commonly seen associated with it: *Alocasia macrorrhiza* (L.) Schott, *Arachnioides rhomboidea* (Wallich ex Mett.) Ching, *Asparagus cochinchinensis* (Lour.) Merr., *Aspidistra daibuensis* Hayata, *Aster taiwanensis*

Kitam., *Begonia laciniata* Roxb., *Carex baccans* Nees, *Colocasia formosana* Hayata, *Cyanotis kawakamii* Hayata, *Elatostema sessile* Forster var. *cuspidatum* Wedd., *Oplismenus undulatifolius* (Ard.) Roemer & Schultes, *Peperomia japonica* Makino, *Pilea kankaoensis* Hayata, *Pilea trinervea* Wight, *Pollia secundiflora* (Bl.) Bakh., *Selaginella delicatula* (Desv.) Alston, *Setaria palmifolia* (Koenig) Stapf, and *Tricyrtis formosana* Baker.

KEY TO THE SPECIES OF BEGONIA IN TAIWAN

The following key is provided to aid in the identification of the ten species of *Begonia* indigenous to Taiwan:

1. Plant acaulescent; inflorescences arising directly from rhizome.
   2. Tepals of pistillate flowers 3 (very rarely 2 or 4); rhizome moniliform; stipules persistent, plant deciduous. ..... *B. austrotaiwanensis.*
   2. Tepals of pistillate flowers 5; rhizome not moniliform; stipules deciduous; plant evergreen. ..... *B. fenicis.*
1. Plant caulescent; inflorescences arising from axils of cauline leaves.
   3. Tepals 2 in both staminate and pistillate flowers; tubers and stolons produced from the erect stem base; plant deciduous. ..... *B. ravenii.*
   3. Tepals 4 in staminate flowers, 5 to 6 (to 8) in pistillate flowers; tubers and stolons lacking; plant evergreen.
      4. Plant with distinct creeping rhizome.
         5. Plant densely pubescent throughout. ..... *B. laciniata.*
         5. Plant glabrous to subglabrous.
            6. Leaves irregularly finely dentate; abaxial wing on capsules rotund to orbicular, 19–26 mm long. ..... *B. chitoensis.*
            6. Leaves laciniate; abaxial wing on capsules nearly triangular, 7–16 mm long. ..... *B. formosana.*
      4. Plant without creeping rhizome.
         7. Plant densely pubescent. ..... *B. buimontana.*
         7. Plant glabrous to subglabrous.
            8. Capsules wingless. ..... *B. aptera.*
            8. Capsules unequally 3-winged.
               9. Mature leaves narrowly lanceolate to lanceolate, 7–14 by 2–4 cm, width/length quotient ca. 1/6–1/3; petiole 2–4 cm long. ..... *B. taiwaniana.*
               9. Mature leaves broadly lanceolate to narrowly ovate, 12–33 by 6–14 cm, width/length quotient ca. 2/5–3/5; petiole 6–26 cm long. ..... *B. lukuana.*

CYTOLOGY

Cytological studies of *Begonia austrotaiwanensis* (see FIGURE 2) reveal n = 18 or 19 in pollen mother cells and $2n$ = 36–38 in root-tip cells. Some interbivalent connections are observed in diakinesis, but the segregation of chromosomes at anaphase appears normal. Three small bivalents and either 15 or 16 larger ones are observed at diakinesis. This is corroborated by the somatic complement that consistently comprises six small chromosomes and 30 to 32 larger ones. It is possible therefore that the somatic chromosome number of *B. austrotaiwanensis* is $2n$ = 36, with the additional one or two large chromosomes observed in some cells being B-chromosomes. The B-chromosomes

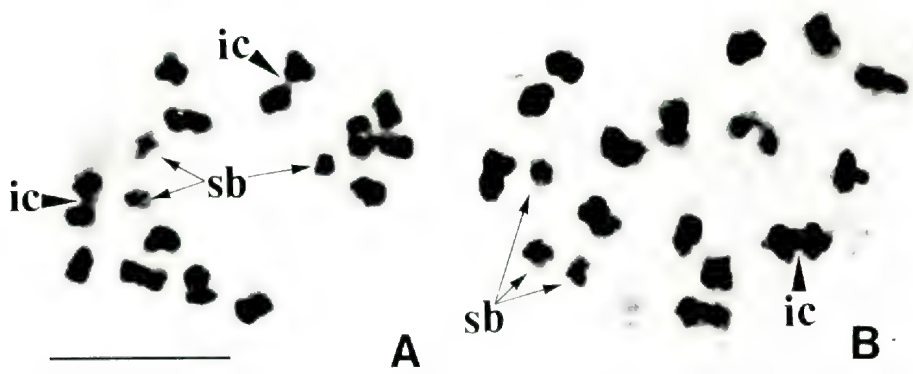


FIGURE 2. Chromosomes of *Begonia austrotaiwanensis* (from *Chen 375*): A, diakinesis, $n = 18$; B, diakinesis, $n = 19$, possibly 18 + 1B. Scale bar = 10 μm; sb = small bivalent; ic = interbivalent connection.

appear to be euchromatic and are not readily distinguishable from somatic chromosomes.

DISCUSSION

Begonia austrotaiwanensis is unique in having the combination of an acaulescent, deciduous habit; a moniliform rhizome consisting of several ellipsoid to subglobose units with persistent stipules; inflorescences arising directly from the rhizome; flowers of both sexes scented, the staminate flowers with four tepals, the pistillate ones with three tepals and two styles; two-locular ovaries; axile placentation; and very unequally three-winged capsules, with the abaxial wing narrowly triangular, erect, and much protruded. Plants of *B. austrotaiwanensis* usually grow on steep, bare, rocky slopes or rock faces with shallow soils, often near seasonal waterfalls or by streams. They are found at elevations between 200 and 800 m along the forest margin in southern Taiwan, an area with a monsoon climate. It is a very distinct species that is often sympatric with *B. laciniata* Roxb., which has a much wider distribution in Taiwan (see MAP 1). *Begonia laciniata* is usually found in the forest or at the forest margin at elevations between 600 and 2100 m. When the two species occur together, *B. austrotaiwanensis* tends to grow higher up on the rocky slopes, whereas *B. laciniata* is usually found at the base of the slope and is frequently intermixed with the abundant herbaceous vegetation.

An examination of *Begonia* specimens deposited at all herbaria in Taiwan reveals that *B. austrotaiwanensis* was not collected until 1986. It was overlooked in the past presumably due to its restricted distribution and because it often occurs together with the widespread *B. laciniata,* from which it is not readily distinguishable at a distance. Since *B. austrotaiwanensis* tends to grow higher up on steep rocky slopes that are relatively inaccessible, plant collectors are likely to ignore it and collect instead the abundant *B. laciniata* at their feet. The fact that *B. austrotaiwanensis* sheds its leaves in the winter also makes it less visible than the evergreen *B. laciniata.*

Traditionally, the number of tepals in staminate and pistillate flowers, the number of styles and ovarian locules, and the placentation type are important characters in delimiting the sections of *Begonia* (Baranov, 1981; Baranov & Barkley, 1974; Barkley, 1972a; De Candolle, 1864; Warburg, 1894). *Begonia austrotaiwanensis* appears to fit in section *Weilbachia* A. DC., which otherwise includes ten species from Mexico and two from Central America (one from El Salvador, one from Guatemala and El Salvador) (Baranov, 1981; Barkley, 1972b, 1972c; Barkley & Baranov, 1972; Barkley & Golding, 1974; Smith *et al.*, 1986; Warburg, 1894). Dieter C. Wasshausen (pers. comm.) suggested placing this new species in the Asiatic section *Platycentrum,* which characteristically has 4 to 6 tepals in the pistillate flowers (*B. austrotaiwanensis* usually has three, very rarely two or four, the fourth much reduced when present). Other than this character, which is evolutionarily labile (L. Brouillet, pers. comm.), *B. austrotaiwanensis* appears to be appropriately placed in sect. *Platycentrum.* Studies of leaf microcharacters of *Begonia* conducted in Brouillet's laboratory showed that sects. *Platycentrum* and *Weilbachia* differ in several traits related to indumentum and anatomy (Brouillet, pers. comm.). Section *Platycentrum* characteristically has leaf emergences with processes and pneumathodes (stomata in lines) on the petiole. By contrast, sect. *Weilbachia* lacks the above characters but has T-shaped glandular hairs and oxalacetic crystals in the leaves. In our study we found that *B. austrotaiwanensis* agrees perfectly in leaf microcharacters with sect. *Platycentrum* and may be appropriately placed in this Asiatic section.

ACKNOWLEDGMENTS

This work was supported in part by a research grant from the Academia Sinica, Taipei, Taiwan, to Ching-I Peng. We thank Shu-Chuan Shaw, Biology Department, National Chengkung University, who first collected a living specimen of *Begonia austrotaiwanensis* from Shanping, Taiwan, in July, 1986, and presented it to the senior author; Nai-Hang Chang, Taiwan Forestry Research Institute, for field assistance at the type locality; and Hsin-Fu Yen, Horticultural Department, National Taiwan University, who identified some of the plants associated with *B. austrotaiwanensis.* We are indebted to Hongya Gu (Center of Life Sciences, Peking University) for providing useful information concerning the mainland Chinese species of *Begonia.* We are most grateful to John D. Dwyer (Missouri Botanical Garden) for assistance with botanical Latin. Luc Brouillet (Institut Botanique de l'Université de Montréal), Dieter C. Wasshausen (Smithsonian Institution), Bernice G. Schubert, and David E. Boufford (both at the Arnold Arboretum, Harvard University) provided useful comments in their reviews of the manuscript.

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A NEW SUBSPECIES OF MALLOTUS OREOPHILUS (EUPHORBIACEAE) FROM SOUTH-CENTRAL CHINA

DAVID E. BOUFFORD[1] AND TSUN-SHEN YING[2]

Mallotus oreophilus subsp. *latifolius* (Euphorbiaceae), which differs from subspecies *oreophilus* in having leaves consistently wider than long, is described as new from Sichuan Province, China.

Mallotus oreophilus Muell.-Arg. subsp. **latifolius** Boufford & T. S. Ying, subsp. nov. FIGURE

Mallotus oreophilus similis sed in foliis latioribus subreniformis vel transverse oblongis differt.

Shrubs or small trees 1.5–13 m tall. Leaves subreniform to oblong, the blades 6–14 cm long, 6.5–20 cm wide, base truncate to very broadly cuneate, apex abruptly short acuminate, upper surface glabrous or with sparse stellate hairs along the main veins, lower surface densely stellate tomentose. Petioles, rachis of inflorescence, flower buds and fruiting capsules densely stellate tomentose. Branchlets glabrescent with stellate hairs.

TYPE: China. Sichuan Province: Dujiangyan Municipality (formerly Guan Xian); between Guanmengzi and Guihuashu, upstream from Longxi along the Longxi River, elev. 1120 m, tree ca. 20 m tall, on moist slope, 3 Sep 1988, *D. E. Boufford & B. Bartholomew 24496* (holotype, PE; isotypes, A, CAS, HAST, IBSC, KYO, L, TI).

ADDITIONAL SPECIMENS EXAMINED. **China.** SICHUAN: Changning Xian, *Chuanjingyi Team 0561* (PE); Emei Xian, *C. Y. Chiao & C. S. Fan 184* (A), *C. L. Chow 6148* (A), *W. P. Fang 7842* (PE), *7843* (PE), *7914* (A, PE), *7915* (PE), *12690* (A, PE), *16497* (A), *16640* (PE), *16897* (A), *18863* (A), *18928* (PE), *K. C. Kuan 710* (PE), *1521* (PE), *Sino-U. S. S. R. Exped. Team 1845* (PE), *2472* (PE), *T. H. Tu 189* (PE), *F. T. Wang 23148* (A, PE), *K. H. Yang 54677* (PE), *54897* (PE), *55595* (PE), *56137* (PE); Guan Xian, *S. Chang 00525* (PE), *Y. S. Liu 1954* (A), *S. S. Chien 5692* (A), *W. P. Fang* 2103 (A), *F. T. Wang 20909* (A); Hongya Xian, *S. Chang 1723* (PE), *T. W. Yao 4060* (PE); Mabian Xian, *F. T. Wang 23096* (A); Pingshan Xian, *Chuanjingyi Team 0607* (PE), *0952* (PE); Tianquan Xian, *S. Chang 01762* (PE), *Chuanjingyi Team 00411* (PE); Ya'an Xian, *C. Y. Chiao 2049* (A), *T. P. Wang 8494* (PE); Yibin Xian, *Chuanjingyi Team 1247* (PE); Yingjing Xian, *T. W. Yao 3762* (PE).

Mallotus oreophilus subsp. *latifolius* differs from the typical subspecies in the shape of the leaf. Subspecies *oreophilus* has the blades ovate to widely ovate, acute to acuminate, and clearly longer than wide; in subspecies *latifolius*

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Journal of the Arnold Arboretum **71**: 575–578. October, 1990.

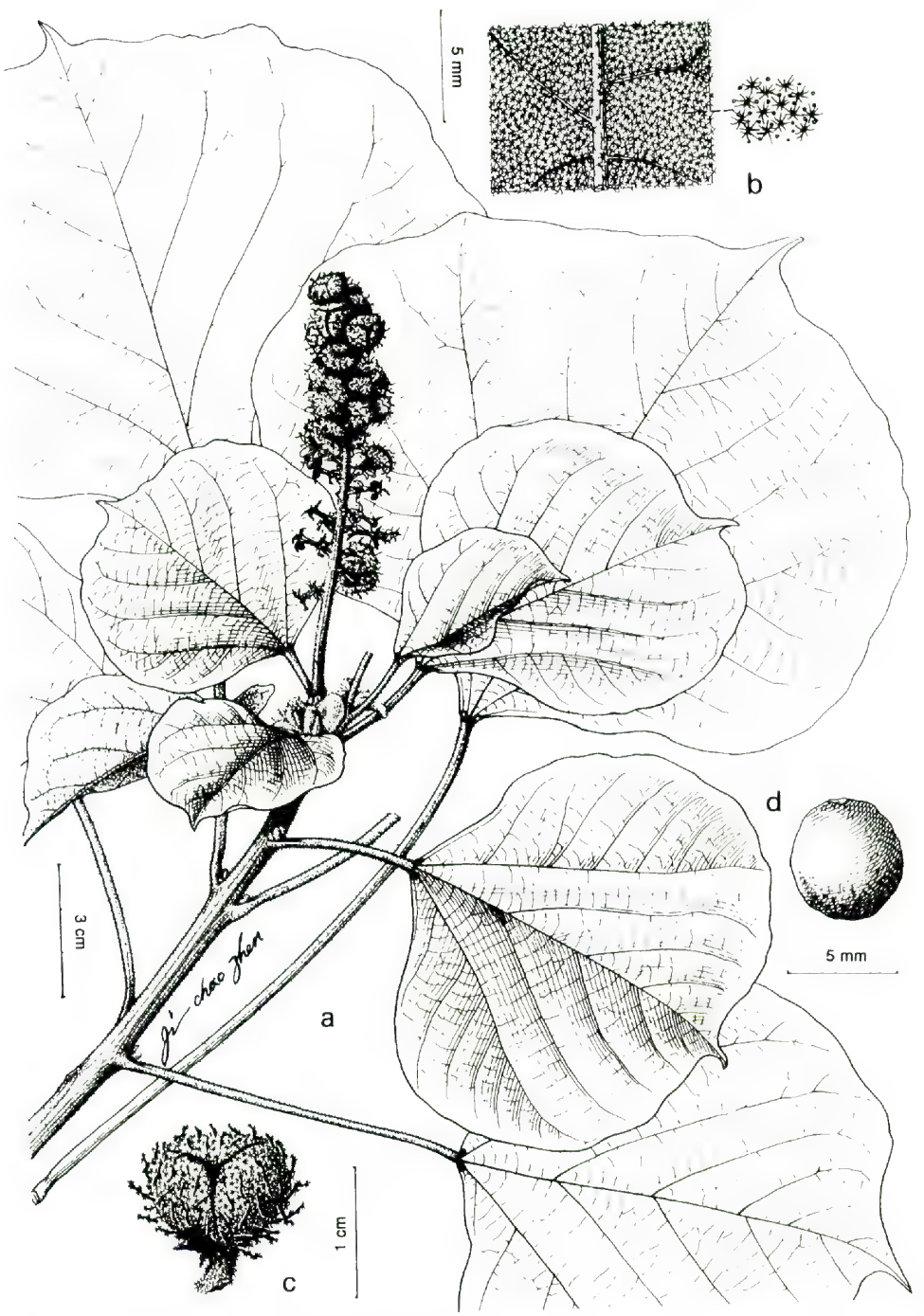

FIGURE. *Mallotus oreophilus* subsp. *latifolius*: a, habit; b, lower surface of leaf showing stellate hairs; c, mature capsule; d, seed. Based on *Boufford & Bartholomew 24496* (PE).

Map of China showing distribution of *Mallotus oreophilus* subsp. *latifolius*.

the leaves are subreniform to oblong and consistently wider than long. The relatively short, acuminate leaf tip in subspecies *latifolius* arises abruptly from the otherwise rounded to subtruncate apical edge of the blade making it quite pronounced. Subspecies *latifolius* occurs in the mountains on the southern and western edge of the Sichuan Basin (see MAP). *Mallotus oreophilus* subsp. *oreophilus* ranges from south-central China through the Himalayan region to the eastern Himalaya (Shaw, 1968).

We have seen a single specimen from Yunnan Province, Mengse [Mengzi] Xian (*A. Henry 10925* (A)), well south of the range of subspecies *latifolius,* that appears intermediate between typical subspecies *oreophilus* and subspecies *latifolius*.

ACKNOWLEDGMENTS

We wish to thank Bruce Bartholomew, Li Gang, Zhu Guanghua, who participated in the fieldwork, Chen Minghong for making the arrangements in western Sichuan in 1988, C. Z. Ji for his beautiful illustration, and the National Geographic Society for its generous support of fieldwork in China.

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BOOK REVIEWS

Tropical Woody Rubiaceae, by E. Robbrecht. *Opera Botanica Belgica* Volume 1. 272 pp. Meise: Nationale Plantentuin van België. 1988. ISBN 90-72619-02-1. Softcover. No price given.

The premier issue of *Opera Botanica Belgica* is the first family-wide summary of the systematics of the Rubiaceae to appear in almost twenty-five years, bringing us up to date in virtually all areas of research bearing on the taxonomy of the fourth largest family of angiosperms (637 genera and roughly 10,700 species). Most of this well organized study describes and evaluates "characteristic features" (especially morphological and anatomical features) of Rubiaceae that have been, or might be, employed by taxonomists. Discussion extends to idioblasts, exudates, crystals, arilloids, ant and mite associations, bacterial and fungal interactions, pollination biology, dispersal biology, biogeography at the generic and tribal levels, and much more. The new classification follows from a re-evaluation of the characters as well as the taxonomic schemes proposed by Schumann (1891), Verdcourt (1958), and Bremekamp (1966). Dr. Robbrecht convincingly argues that division of the family into four subfamilies and more than forty tribes yields an improved alignment of morphological and anatomical data that is also supported by chemical and cytological information, as scanty as that often is.

Woody Rubiaceae are emphasized, but herbaceous (and mostly temperate) taxa are included in the proposed classification, which extends to the entire family. Herbaceous species are present in less than 20 percent of rubiaceous genera, and their repeated derivation from woody ancestors is evident. Another admitted bias is toward Old World (especially African) genera, and the subfamily Ixoroideae, which is where the author has much research experience, and where our knowledge of the family is thus relatively far advanced. Robbrecht's reliance on floristic as well as monographic research is evident throughout, and one senses that years of "routine" herbarium identifications have contributed substantially to his comprehensive view of character distribution in the family.

The discussion of "characteristic features" is presently the most reliable and accessible exposition of morphological and anatomical variation in the Rubiaceae. Terminology pertaining to trichomes, the wall structure of exotesta cells, colleters, and inflorescences is expanded and clarified. For example, the anomalous "hairs" on *Hillia* seeds are shown to be highly divided wings. The discussion is thorough and unambiguous, an exception perhaps being the distinction between "fang" and "climbing" hooks in some lianas (if indeed they are different structures), and the characterization of *Airosperma* as having corolla lobes contorted to the right, an error apparent in Schumann's original illustration where both left- and right-contorted corollas are figured.

The author often suggests the adaptive significance of characters, although

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where data are slim the conclusions are necessarily tentative. Robbrecht does not over-speculate, and for a few systematically significant features—such as ovule number or exotesta cell anatomy—he advances no adaptive explanation. Is there a correlation between seed coat anatomy and fruit type, perhaps?

The taxonomic value or "reliability" of characters in distinguishing genera, tribes, and subfamilies is illustrated with reference to their use in prior systematic studies. The many characters deemed useful only at lower taxonomic ranks are, of course, those that exhibit strong homoplasy among the tribes. Other potentially useful characters, such as stipule ontogeny and vascularization, pollen, and fruit-production strategies, are still insufficiently known to be of much systematic value at the tribal level.

Homoplasious evolution is also strongly suggested for many characters when they are mapped against the author's proposed classification in a series of Venn diagrams. This mapping method, where tribes are represented by circular shapes, allows the "placing" of taxa in the system without implying a specific phylogeny. Probable instances of convergence include reduction in the number of ovules per ovary locule and presence of raphid crystals—characters that served as the basis for subfamilial circumscription by Schumann (in the case of ovule number) and by Verdcourt and Bremekamp (for raphides). Other instances of convergent or parallel evolution include tetramerous flowers, a tendency for increase in flower parts (pleiomery), corolla lobe aestivation, dioecism and heterodistyly, and development of a stylar pollen-presentation mechanism. The parallel evolution of small fruits in both Old and New World Gardeniineae is an example of how data from floristic studies contribute to evolutionary hypotheses.

Robbrecht's classification purports to delimit "natural" taxa, and is "evolutionary" in the sense that paraphylesis is accepted while polyphylesis is not; he considers phylogenetic classification of Rubiaceae to be an eventual goal. (Garcia Kirkbride's (1982) phylogeny of Rubiaceae subfamilies based on two characters, and Bremer's (1987) study of Argostemmateae and Hamelieae are among the very few explicitly cladistic investigations carried out for Rubiaceae.) Robbrecht emphasizes taxa that are "intermediate," linking higher groups, when discussing relationships. He accepts the supposition (F. Hallé, 1967) that Ixoroideae are the most primitive subfamily, but further phylogenetic speculation is limited (indeed, "phylogeny" does not appear in the index), although evolutionary trends are hypothesized for nodal anatomy, stipules (four per node is primitive and rare), and habit (herbs are advanced). Placental evolution is outlined for Hedyotideae (from phyllospory to stachyospory) and for Rubioideae (from pluriovulate to uniovulate placentas). For broader phylogenetic hypotheses, the available data base seems yet inadequate.

Looking for overall correlations among characters, Robbrecht abandons the single-character criteria previously employed to align genera and tribes. The result is a scheme that resembles Schumann's classification in some important respects, but cannot be considered a return to the "classical" systems of the nineteenth century. Bremekamp's small, segregate subfamilies are rejected, as is Verdcourt's apparently unwarranted reliance on raphid crystals as the pri-

mary defining feature of Rubioideae. Two examples give an idea of the extent of Robbrecht's rearrangements, as well as the rationale informing them.

Subfamily Rubioideae contains, "without doubt, the most advanced members of the family," i.e., the largely herbaceous tribes. The subfamily includes all tribes assigned there by Bremekamp, except Knoxieae and Craterispermeae (moved to Antirheoideae), as well as Ophiorrhizeae (placed by Bremekamp in Urophylloideae), and Pomazoteae (placed in its own subfamily by Bremekamp). While possession of raphids was essential for membership in Rubioideae in the systems of Verdcourt and Bremekamp, Robbrecht points out that it cannot stand alone as a defining feature, since species possessing raphides are manifestly related to others without them. Robbrecht identifies multiovulate and uniovulate tribes as comprising two major groups within the subfamily, the uniovulate group being the more "natural" (monophyletic?), but some Morindeae—usually with one ovule per cell—may sometimes have two. The Hedyotideae "indicates that a link between the two [tribal groupings] seems plausible. This same tribe seems to link the subfamily Rubioideae with the Cinchonoideae, viz. the Isertieae." The tribes Anthospermeae, Paederieae, Theligoneae, Spermacoceae, and Rubieae show a trend toward dry fruits as well as herbaceous habit.

Subfamily Antirheoideae is the most heavily emended of Bremekamp's and Verdcourt's subfamilies—by them restricted to tribe Guettardeae—but here greatly expanded to include Alberteae, Knoxieae, Vanguerieae, and Chiococceae, these last tribes distributed to other subfamilies by Verdcourt and Bremekamp on account of presence of raphides or appreciable endosperm. Robbrecht's Antirheoideae is essentially a reconstruction of Schumann's [supertribe] "Guettardinae," members of which "show so striking similarities in their flowers and fruits, that Bremekamp's and Verdcourt's dispersal of the "Guettardinae" over different subfamilies resulted, no doubt, in a more artificial classification." To this re-expanded subfamily Robbrecht also assigns the Retiniphylleae, Cephalantheae, and Craterispermeae.

The gaps in our rubiaceous knowledge are many and wide, and Robbrecht calls for survey-type studies to establish the limits of tribes Cinchoneae, Condamineae, Rondeletieae, and Isertieae. In the Antirheoideae, the tribal position of many genera is uncertain, and this is also true for Psychotrieae, where delimitation of the enormous *Psychotria* is a problem. Modern revisions are lacking for many genera, and our knowledge is uneven geographically. The least well known Rubiaceae are in Malesia and Madagascar, where groups often have an important bearing on an understanding of African and Asiatic taxa. Concerning Madagascar, the study of Rubiaceae is "practically dormant" while relentless deforestation results in the continuing loss of species. The study of Australian and New Caledonian Rubiaceae is said to be in a similarly quiescent state. In the *Flora Neotropica* series, a single monograph (on the three genera of Henriquezieae) has appeared—more quiescence.

Perhaps only a fragment of living tropical woody Rubiaceae will be saved for future investigation, but an enormous and hardly exploited resource of evolutionary data is already present in systematic collections. Robbrecht shows

us how those data can be extracted and what we should be looking for. As a minimal data set that should be assembled for the whole family (presumably for all genera) he suggests the following: presence or absence of raphides; anatomy of external hairs; corolla aestivation; data on floral biology; anatomy of seed exotesta; and pollen type (position, number, and type of apertures and features of the exine). This is, of course, far from what might be achieved with concerted and coordinated effort, namely an exhaustive, accessible, perfectly comparable, and thoroughly vouchered data base for Rubiaceae worldwide. The present study makes it plain that a lot of information can be gathered using the simplest techniques.

As a reference work, Dr. Robbrecht's monograph is excellent. In the exposition of his proposed classification, he gives the principal features of each suprageneric taxon, references to previous studies bearing on tribal classification, and a summary of geographical distribution. All included genera are listed for each tribe and subtribe. Among the appendices is a list of all accepted generic names and synonyms with tribal assignment—the first such published index in nearly a century. The bibliography of about 300 references includes the pages where each is mentioned in the text (a very useful feature), and in the subject index the main place of discussion is set in bold type. The taxonomic index also includes page references to Schumann, Verdcourt, and Bremekamp. Typographical errors are few, and I found only two cited references omitted from the bibliography. Commenting on the task of assembling and arranging so much material, the author admits that the Rubiaceae are "so vast a family that a single researcher cannot hope to gather all essential taxonomic data for an in-depth analysis." But some researchers are evidently better equipped to do so than others. Addressing Volken's question of how Schumann's great productivity might be explained, Stafleu and Cowan (1985) suggest that "a really convincing and comprehensive answer is not possible." Schumann's industry, and that of his successors in Rubiaceae systematics—Verdcourt, Bremekamp, and Robbrecht—is an inspiration.—S. P. DARWIN, Department of Biology, Tulane University, New Orleans, Louisiana 70118.

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Wayside Trees of Malaya, by E. J. H. Corner. ed. 3. Kuala Lumpur: The Malayan Nature Society, 1988. 2 volumes, 861 pp., *236 plates,* & *260 figures.* ISBN 967-99906-0-5. Hardcover. No price given.

Out of print for decades, that triumph of natural history, the *Wayside Trees of Malaya,* has now appeared in a new edition.

The *Wayside Trees* describes the commonly cultivated species and the frequently encountered indigenous trees of one equatorial country, but its value is global. Professor Corner pioneered the objective description of tree shape, bark morphology, and mode of growth. His observations on phenology and reproductive biology are still unexcelled; his narrative remains provocative and totally absorbing.

The form and content of the original 1940 edition remain essentially unchanged, though it is a little sad that the quality of printing has declined, particularly with respect to the illustrations. Nomenclature has been meticulously checked. The accounts of several families are now illuminated by the author's "Durian Theory," to which his researches on Malaysian trees gave birth. Other new information includes Hallé and Oldeman's on tree branching patterns, Koriba's on modes of growth, and Medway's on phenology. The essay on the natural history of figs is embellished with fascinating additions. The section on trees of local interest has been brought up to date and expanded with the author's astute eye and acerbic wit.

By and large the family and species descriptions stand firm also. This is because they remain based on opinion derived from Corner's own field observations within one country. Generally, his family and generic concepts are broader, and his species narrower than are currently common in the Far East, concepts that are under the spell of "Flora Malesiana." Nevertheless, the Bombacaceae are now separated from the Malvaceae, and the Moraceae and Ulmaceae from the Urticaceae (where *Streblus* becomes four genera); the Anisophylleaceae are retained; but *Ixonanthes* and *Erythroxylum* are kept together on the basis of their seed structure; *Irvingia* remains in the Simaroubaceae; the Chrysobalanaceae in the Rosaceae; and *Duabanga* and *Sonneratia* in Lythraceae. Various satellites of the Euphorbiaceae are retained in that family. The original generic definitions and names in such families as the Rosaceae (Chrysobalanaceae), Apocynaceae, Rubiaceae, and Leguminosae, where they have been under recent fissiparous scrutiny, have been maintained. Langsats and dukuns are placed in one species, as are the forms of *Allophyllus,* but not those of *Pometia.* This is the work of someone who knows the plants and only makes changes when personally convinced.

Everywhere, Corner's continuing love of Malaya, its people, and its forests shines through the text. Considering the more than forty years of change of old forests to plantations, lanes to superhighways, and villages to cities that have elapsed, it is not surprising that many of the trees originally illustrated have gone. Amazingly, some also remain—it is always fascinating to learn how they

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Journal of the Arnold Arboretum **71:** 583, 584. October, 1990.

have survived. This should challenge the Malayan Nature Society to search for others that are still alive.

As testimony of the continuing value and majesty of this masterpiece to the public, the embarking graduate student, and the experienced scientist alike, the following is taken from a new passage in the introduction to the Dipterocarpaceae: "When we look upon the lowland forest or gaze up into its vaults, we see the canopy of dipterocarps whose sombre crowns compose very largely the ocean of trees that once covered the Malay Peninsula. . . . This glorious spectacle has been whittled away in the course of civilization, decimated this century by commercial logging, and now, with urban demand for agriculture, it is in danger of disappearing. Vast trunks thunder along highways to saw-mills, apparently from nowhere, and revenue accrues, but where can the citizen, the biologist, or the visitor see these fabulous giants—the most majestic trees that any land produces? One would have thought that such a national heritage should have been guarded zealously. There remain, fortunately, some tracts of this lowland forest preserved in catchment areas, national parks, forest reserves and game reserves though, as the shortage of timber increases, they may be deprived."—P. S. ASHTON, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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HARVARD UNIVERSITY VOLUME 71 1990

Dates of Issue

No. 1 (pp. 1–144) issued 25 January 1990.
No. 2 (pp. 145–274) issued 5 April 1990.
No. 3 (pp. 275–390) issued 9 July 1990.
No. 4 (pp. 391–604) issued 11 October 1990.

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Journal of the Arnold Arboretum *October, 1990*

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